ALPINE GRASSHOPPERS (ORTHOPTERA: ACRIDIDAE) IN THE SOUTHERN ALPS OF CANTERBURY, NEW ZEALAND

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INTRODUCTION

1.1 Introduction and Review of the Literature

Grasshoppers of the family Acrididae are typically lowland insects. In New Zealand, however, these grasshoppers are a very obvious constituent of the alpine biome and are considered to be an important factor in the biology of this area. Bigelow (1967) recognized 15 species of acridids in New Zealand. Twelve of these are alpine and inhabit the vegetated and scree areas above treeline. They may descend to lower altitudes where forest is absent, but are seldom found below 3000 ft. This preponderance of alpine species is a distinctive feature of the New Zealand grasshopper fauna.

In New Zealand much of the mountain land bears the scars of erosion. This is particularly true in Canterbury where the mountains are characteristically shingle scree above an altitude of about 5000 ft. Grasshoppers are obvious inhabitants of this environment, and as phytophagous insects are possibly contributing towards erosion. Before the significance of any relationship between alpine grasshoppers and alpine vegetation or high country erosion can be determined it is necessary to know more about the biology of the grasshoppers.

The taxonomy of the New Zealand alpine grasshoppers was recently revised (Bigelow, 1967). Their biology, however, has been comparatively neglected. The present study is a comparative investigation of aspects of the biology of five species of

alpine grasshoppers:

Brachaspis collinus (Hutton)

Brachaspis nivalis (Hutton)

Paprides nitidus Hutton

Sigaus australis (Hutton)

Sigaus villosus (Salmon)

The study of these species was limited to three study areas in the Southern Alps of Canterbury, New Zealand. Two of the species are restricted to scree, two to vegetated areas and one can live in both habitats. Four of the species are present in more than one study area. It has, therefore, been possible to make comparisons between species, between species with different habitat preferences and between different local populations of a single species. The data used in this study were obtained from the examination and dissection of preserved grasshoppers, and from laboratory and field observations and experiments.

Literature on the biology of the New Zealand alpine grasshoppers is limited. Batcheler (1967) published preliminary observations on *Brachaspis collinus* at Cupola Basin, Nelson. Although primarily concerned with the bionomics of *B. collinus*, he also discussed aspects of its biology. He suggested that *B. collinus* has a very flexible life cycle with development from hatching to maturity probably taking about three years, with most stages including adults capable of overwintering, and with oviposition occurring at any time during the snow-free season.

Batcheler also considered that B. collinus adult females at Cupola Basin laid only one pod of eggs before dying, and that eggs laid early in the season hatched before the following winter. The present study indicates that B. collinus at Temple Basin has a flexible life cycle as Batcheler concluded, but that adult females probably lay more than one pod of eggs before dying and that all eggs go into an obligatory diapause.

Gonad structure, egg pod structure and egg development have all been neglected by previous workers. Parasites, except for a brief reference to external mites by Batcheler (1967) and to gordian worms by Marples (1962), have also been neglected.

Recently Watson (1971) examined the feeding behaviour of alpine grasshoppers in the Craigieburn Range of Canterbury, New Zealand.

Other literature on the New Zealand alpine grasshoppers is concerned with their taxonomy, size variation or evolution. The original descriptions of most of the New Zealand grasshoppers were made by Hutton (1897 and 1898). Apart from a paper by Salmon (1950), their taxonomy remained untouched until revised by Bigelow (1967) who also reviewed their distribution and discussed their geographical and altitudinal size variation. Bigelow's work has encouraged much of the subsequent work on New Zealand grasshoppers. Irving (1967), on the basis of additional material she examined, made minor adjustments to some of Bigelow's species ranges. The nymphal instars of the alpine grasshoppers were

described by Hudson (1967 and 1970). One of the taxonomic problems noted by Bigelow (1967), geographical variation in notch width of the female subgenital plate of Paprides nitidus, was investigated by Peterson (1968). A brief review of the state of grasshopper taxonomy was made by Johns (1970). The present study provides additional data on geographical variation, nymphal instars, and inter- and intra-specific variation in femur length, pronotum length, gonad structure, egg pod structure and egg size.

The New Zealand alpine grasshopper species which has been most studied is Brachaspis collinus. In addition to the work of Batcheler (1967), Staples (1967) has investigated colour polymorphism and altitudinal variation in size in this species at Temple Basin, and Green (1967) has investigated its colour polymorphism at Cupola Basin.

The evolutionary history of the New Zealand alpine grasshoppers has been discussed by Bigelow (1967), Irving (1967), Peterson (1968) and Dumbleton (1970). All expressed the opinion that the present distribution pattern of grasshoppers is a result of the evolution and dispersal of populations isolated during the Pleistocene glaciations. The writer accepts the conclusions of these authors and does not propose to discuss speciation. The pre-Pleistocene history of the grasshoppers, however, has not been discussed, except by Bigelow (1967) who very tentatively suggested they may have had a long history of dwelling in alpine regions. Observations made during this study support these views of Bigelow.

Acridids are a world wide group of considerable importance as agricultural pests. As a result, published literature on the group is voluminous. Work in the field was reviewed by Uvarov (1928), and the first volume of a major revision of this book (Uvarov, 1966a) has been published. The 1928 publication has a very broad coverage, but the 1966 publication covers only morphology and physiology; therefore there is to date no recent review of the ecology or parasitology of grasshoppers.

Most of the work on alpine grasshoppers in the Northern Hemisphere has been restricted to studies of distribution and taxonomy; very few papers deal with biology and ecology. Alexander and Hilliard (1964) described the life history of the high altitude grasshopper Aeropedellus clavatus (Thomas) in Colorado (U.S.A.). This species exhibits many adaptations allowing it to complete development from hatching to maturity and then death in one season. Its life cycle is abbreviated to four juvenile instars, hatching of its eggs can occur when there is snow and ice in the immediate surroundings, sexual maturation is reached in about six weeks and egg diapause termination appears to take more than one winter. Alexander and Hilliard (1969) described the altitudinal and seasonal distribution of 94 species of Orthoptera in the Rocky Mountains of Colorado. This paper was primarily concerned with distribution, but it did make some relevant statements about the adaptations of Orthoptera to an alpine environment. They suggested that the development of Aeropedellus clavatus was

relatively quicker at higher altitudes. They stated that most species had one year life cycles, overwintering in the egg and maturing the following season, that extended diapause (requiring more than one winter for termination) occurred in some species and that some species overwintered in a juvenile instar. They suggested that an extended diapause facilitated hatching earlier in the season and was thus an adaptation to the short growing period of the high altitude environment. Extended diapause in three species of grasshoppers from a high altitude in the northern Rocky Mountains was noted by Kreasy (1960). Van Horn (1965) found that both sexes of the grasshopper Melanoplus dodgei (Thomas) in the Colorado Front Range decreased in size with altitude. This also appears to be an adaptation to alpine areas because the high altitude grasshoppers would expend less energy on growth and, therefore, require less energy to reach sexual maturity than the lowland forms.

In Europe Dreux (1961) examined the distribution, ecology and biogeographic relationships of the Orthoptera in the French Alps. He noted that most grasshoppers completed their development from hatching to maturity and death in one season. He expressed the opinion that this was because the winter was too cold for the adults to survive. In Yugoslavia Stevanovic (1961) studied the ecology and population dynamics of Aeropus sibiricus L. from the mountains of south west Serbia. A. sibiricus is a close relative of Aeropedellus clavatus (Alexander and Hilliard,

1964) and has a wide distribution across northern Europe and Asia. Like Aeropedellus clavatus, Aeropus sibiricus has only four nymphal instars, but differs in that hatching occurs after only one winter as an egg.

The available literature suggests that most of the Northern Hemisphere alpine grasshoppers, although they may spend more than one winter in the egg stage, develop from hatching to maturity and death in one season. Their adaptations to the alpine environment appear to be: abbreviation of life cycles by a reduction in the number of juvenile instars, attainment of maturity at a smaller size, physiological adaptation to the alpine environment, and perhaps extended egg diapause. Subsequent information will show that the New Zealand alpine grasshoppers have adapted in quite different ways to their alpine environment.

A general study of high altitude insects has been made by Mani (1968). In this book Mani devotes a considerable amount of space to an excellent discussion of the adaptations of insects to the high altitude environment.

1.2 Study Areas

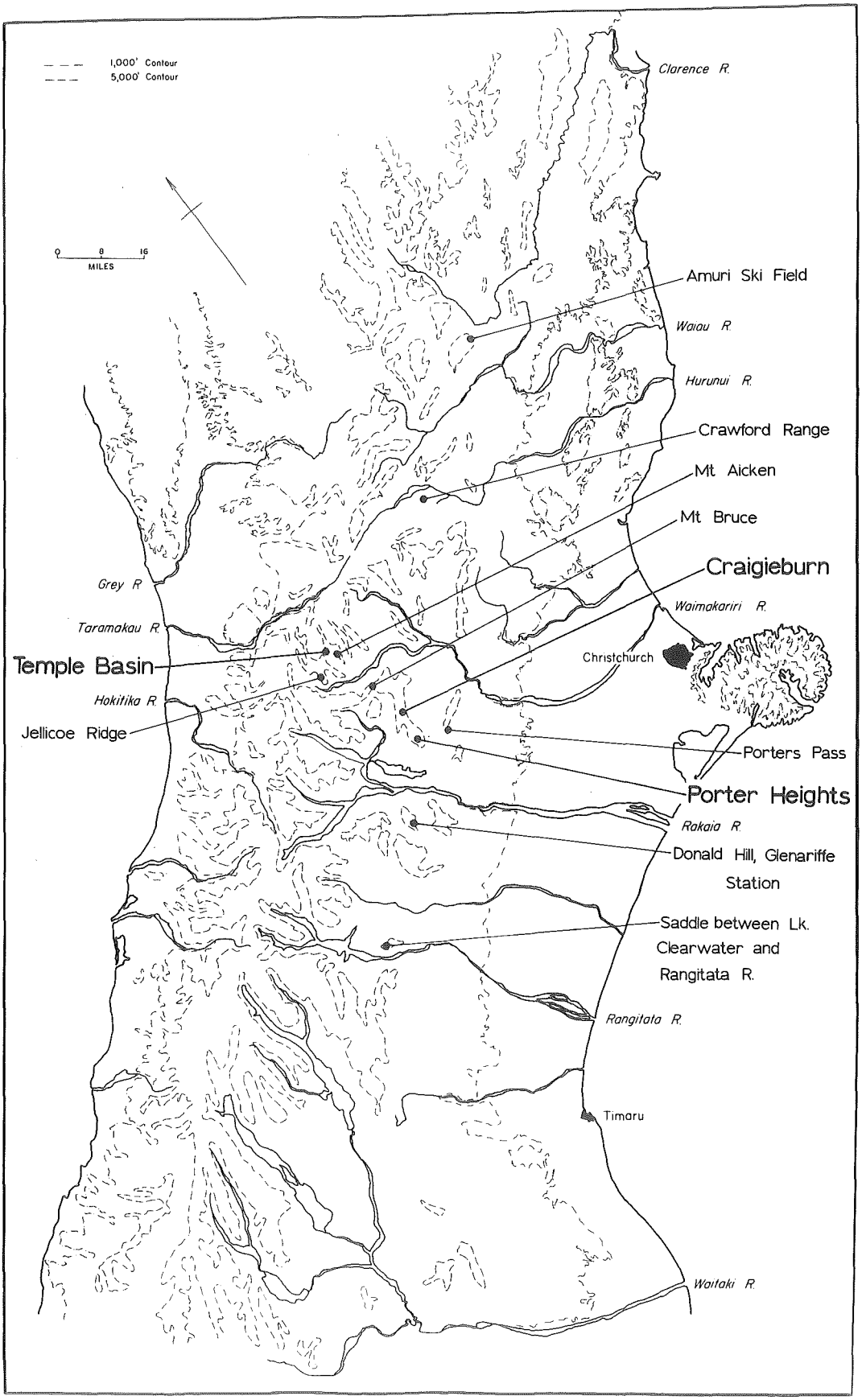
Grasshoppers were collected from three study areas: Craigieburn, Porter Heights and Temple Basin. Their locations are shown in Fig 1.2.1. All three are in the Waimakariri River

catchment at about 43° south latitude. A general study of this catchment, with an excellent bibliography, has been published by the Tussock Grasslands and Mountain Lands Institute (Hayward, 1967). General information about the study areas and surrounding regions can also be obtained from many of the contributions to The Natural History of Canterbury edited by Knox (1969).

The topography of the study areas has resulted directly from glacial and postglacial action on the parent greywacke. Extensive erosion is typical of Canterbury high country (see Fig 1.2.2), most land above 5000 ft being scree.

For the purpose of this study only two alpine habitats will be recognized: screes and vegetated areas (Fig 1.2.3). Screes were defined by Salmon (1968) as "bare stone areas sparsely populated with highly adapted plants". In many cases the plant population appeared to be negligible, but the presence of grasshoppers indicated that some plant material must have been present. Stone size and scree stability varied considerably, with plant density usually being greater on the more stable screes. Vegetated areas carry a reasonable density of plants, and in practice were clearly differentiated from scree areas. The nature of the vegetation varied between study areas and with altitude. The most obvious plants were usually tussocks (Chionochloa sp.).

Porter Heights is at the eastern end of the Craigieburn Range and at the eastern margin of the Southern Alps. It has


1,000' Contour
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MILES
Clarence R.
Amuri Ski Field
Waiau R.
Hurunui R.
Crawford Range
Mt Aicken
Mt Bruce
Craigieburn
Grey R.
Waimakariri R.
Taramakau R.
Christchurch
Temple Basin
Hokitika R.
Jellicoe Ridge
Porters Pass
Porter Heights
Rakaia R.
Donald Hill, Glenariffe Station
Saddle between Lk. Clearwater and Rangitata R.
Rangitata R.
Timaru
Waitaki R.

Figure 1.2.1

Map showing location of places referred to in text.

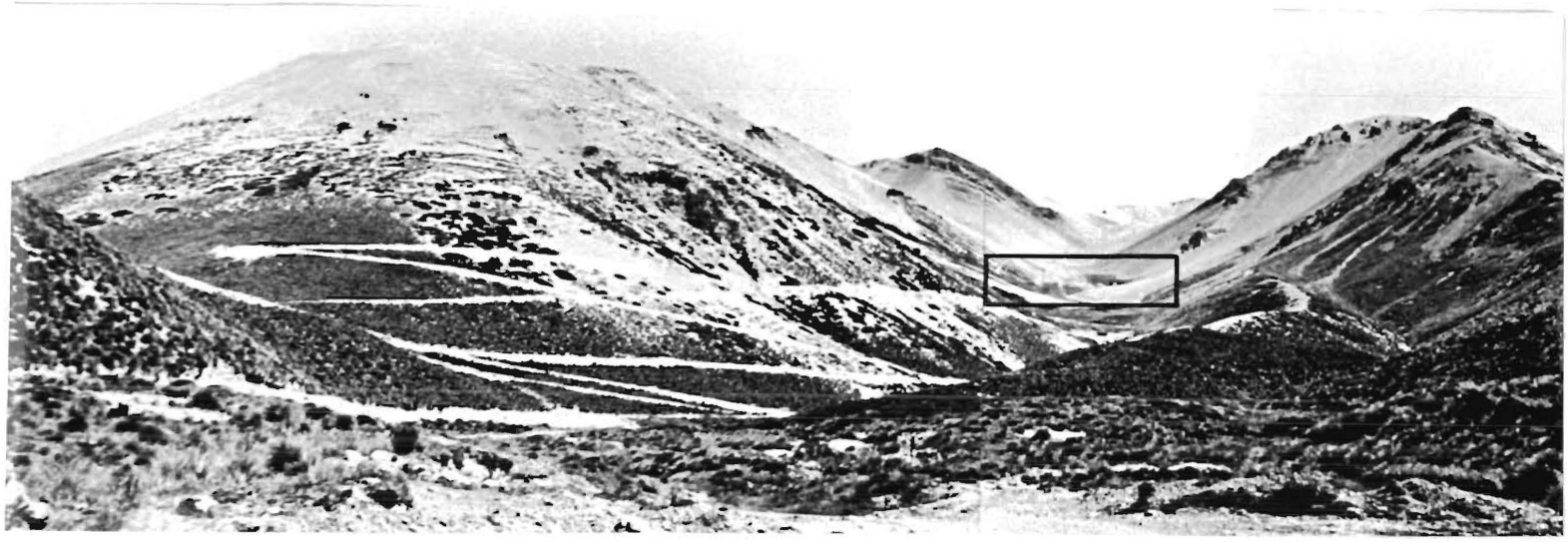


Figure 1.2.2

Porter Heights study area (encircled) and surrounding terrain.

Figure 1.2.3

Photograph taken at 4400 ft at the Porter Heights study area to illustrate difference between scree and vegetated areas.

extensive areas of scree extending from the tops of the surrounding peaks and ridges (6000 to 7200 ft) down to 4500 ft (Fig 1.2.2). The vegetation consists of dense stands of snow tussock (Chionochloa sp.) and large clumps of Cassinia (Fig 1.2.3). There is no forest in this area.

The Craigieburn study area is in a Forest Park in the Craigieburn Range and is the site of the Cave Stream field station of the New Zealand Forest Service. Most grasshoppers were collected from the areas known as Camp Creek Basin (4300 to 5000 ft) and Remarkable Ridge (approximately 5900 ft). In this study area mountain beech forest (Notofagus solandri var. cliffortioides) covers the slopes up to an altitude of 4000 to 4400 ft. Above the treeline are areas of tussock grassland which extend tongues upward into the scree above. The main constituents of the grassland are the snow tussocks (Chionochloa sp.) which are interspersed with many smaller plants; the more important of these being Aciphylla sp. and Celmisia sp.

Temple Basin is on the main divide of the Southern Alps, in Arthurs Pass National Park, three miles to the west of Arthurs Pass township. The study area is a series of three basins extending from 4400 ft to the ridge at 6300 ft. Most collections were made in the Bottom Basin which extends from 4400 to 5100 ft. In this area the vegetation is tussock grassland. The tussocks (Chionochloa sp.) are shorter and the grassland contains a higher proportion of broad-leafed plants (the principle genera being

Celmisia and Anisotome) than the grasslands at Porter Heights and Craigieburn. Temple Basin has many small screes completely surrounded by vegetation. In the immediate area there is no forest.

1.3 The Alpine Climate

The Canterbury climate is discussed by de Lisle (1969), and the climate in the Waimakariri River catchment by Hayward (1967). The Forest and Range Experimental Station of the New Zealand Forest Service has been recording climatic data from the Cave Stream area of the Craigieburn Range (site of the Craigieburn study area), since 1961. Consequently, the records for this area are very good. Morris (1965) discusses the results of the first three years recordings, and the results for the years 1966, 1967 and 1968 are summarized by Apse (1967, 1968 and 1969). Detailed studies of the New Zealand mountain climate are, however, rare. Climatic records for the Porter Heights and Temple Basin study areas are inadequate or non-existent, making comparison between the areas very difficult.

The New Zealand mountain climate is oceanic. Published material (Apse, 1967, 1968 and 1969; Mark, 1965; Morris, 1965; Coulter, 1967) shows that temperature decreases and precipitation increases with increasing altitude. In general, seasonal

temperature change is not great, although the diurnal range of temperature may be quite high. Snow and frosts may occur at any time during the year.

The weather in the study areas varies from year to year. In 1967 very little snow fell, in 1968 an enormous amount of snow fell and 1969 was an approximately "normal" year. Despite this variation, a brief consideration of the weather throughout a "normal" year is worthwhile. Permanent winter snow can seldom be expected before June. The thaw usually starts in September, but the study areas are seldom snow free before late October. The month of November is usually wet. The weather is generally warm in December, January and February and sometimes March. By April, snow, which may lie on the ground for several days, is not uncommon. Mean monthly air temperatures for two alpine areas in the Canterbury region of New Zealand are recorded in Table 6.1. The temperature beneath the snow was found by the author to be constant at about $0^{o}C$.

The prevailing wind in the Canterbury region is the north-westerly, which comes off the Tasman Sea, drops most of its moisture on the western side of the Southern Alps and sweeps across the eastern plains as a warm, dry, fohn wind. Precipitation in the mountains is, therefore, higher in the west and decreases towards the east. Table 1.3.1 shows the mean annual precipitation at three stations chosen for their proximity to the study areas. Temple Basin, like Arthurs Pass, has high

precipitation because of a rain shadow effect. Measurements made during this study suggest that the precipitation at Temple Basin is not greatly different from the 180 inches mean annual precipitation at Arthurs Pass. Craigieburn Ski Basin, with a mean annual precipitation of 73 inches, is drier than Temple Basin. No climatological data exist for the Porter Heights study area, but observations suggest that it has very similar weather to Foggy Peak (just above Porters Pass) for which Molloy (1963) recorded an annual precipitation of about 40 inches. Craigieburn and Porter Heights receive much of their precipitation on a southerly wind, while most of the precipitation at Temple Basin comes from the north-west.

Table 1.3.1: Mean annual precipitation

Site	Altitude (feet)	Precipitation (inches)	Source
Arthurs Pass (township)	2200	180	Hayward (1967)
Craigieburn Ski Basin	5000	73	Morris (1965)
Foggy Peak Ridge (Porters Pass)	3500 and 4500	40	Molloy (1963)

1.4 The Grasshoppers

1.4.a Introduction

Five grasshopper species, belonging to three genera, are considered in this study: Brachaspis collinus (Hutton), Brachaspis nivalis (Hutton), Paprides nitidus (Hutton), Sigaus australis (Hutton) and Sigaus villosus (Salmon). The identification of adults follows Bigelow (1967). The numbering and identification of instars follows Hudson (1970). As her system is not sequential but is based on equivalent developmental stages it is presented in Table 1.4.1

Table 1.4.1: Numbering of instars. (X means that the instar indicated is present.)

Species	Sex	Instar								Moult No.*
		I	II	IIIA	IIIB	IV	V	VI	Adult	
Brachaspis collinus										
	Male	X	X	X		X	X	X	X	6
	Female	X	X	X	X	X	X	X	X	7
Brachaspis nivalis										
	Male	X	X	X		X	X	X	X	6
	Female	X	X	X	X	X	X	X	X	7
Paprides nitidus										
	Male	X	X			X	X	X	X	5
	Female	X	X		X	X	X	X	X	6
Sigaus australis										
	Male	X	X			X	X	X	X	5
	Female	X	X		X	X	X	X	X	6
Sigaus villosus										
	Male	X	X	X		X	X	X	X	6
	Female	X	X	X	X	X	X	X	X	7

* The number of moults does not include the intermediate moult from the vermiform larva to the first instar grasshopper.

Bigelow considers that all species probably belong to subfamily Catantopinae of the Acrididae.

All five species are, in general, restricted to above the treeline (approximately 4000 ft). Where the treeline has been lowered, naturally or artificially, they may descend to lower altitudes, but seldom lower than 3000 ft. Table 1.4.2 summarizes the distribution of the grasshoppers among the three study areas and states the habitat preference of each species.

Table 1.4.2: Distribution of species among study areas, and habitat preferences.

Species	Study Areas			Habitat	
	Craigieburn	Porter Heights	Temple Basin	Scree	Vegetated
Brachaspis collinus			X	X	X
Brachaspis nivalis	X	X		X	
Paprides nitidus	X	X	X		X
Sigaus australis	X	X			X
Sigaus villosus	X	X		X	

Only one species (Paprides nitidus) is found in all three study areas. Two species (Paprides nitidus and Sigaus australis) inhabit vegetated areas, two are confined to screes (Brachaspis

nivalis and Sigaus villosus) and one (Brachaspis collinus) lives in both habitats.

All of the grasshoppers have a similar general form (see Fig 1.4.1 and frontispiece). They are robust and have very reduced wings. They are all diurnal. Development from hatching to maturity appears to take three to four years. All the members of one species in a study area are here regarded as a population.

1.4.b Brachaspis collinus (Hutton)

Brachaspis collinus is a large grasshopper, unique among New Zealand species because it inhabits both tussock and scree. This species shows a wide range of colour polymorphism (Staples, 1967 and Green, 1967). In adults, ground colour varies from grey to bright green. A pair of dorsal longitudinal yellow stripes covering the head and thorax only, or more commonly the head, thorax and abdomen, may or may not be present. The species ranges from northwest Nelson to, approximately, the north side of the Waimakariri River (Bigelow, 1967); thus, at Temple Basin it is near the southern extent of its known range.

At Temple Basin the species has been collected at altitudes as low as 3600 ft but is not abundant below 4500 ft. Above 5500 ft only scree is present and grasshopper density decreases. Specimens have been collected at 6300 ft (the upper limit of collections in this area), but the species probably occurs higher.

Figure 1.4.1

Adult male Brachaspis nivalis. Photograph, J. T. Darby.

Brachaspis collinus is noticeably abundant at scree edges; consequently, some of the best collecting sites are the small screes surrounded by vegetation.

1.4.c Brachaspis nivalis (Hutton)

Brachaspis nivalis is found on screes only. It is generally entirely grey, except for the pink ventro-internal face of the hind femora; but, occasional specimens, of all stages, were found bearing a pair of longitudinal stripes on the dorsal surface of the pronotum.

This species ranges in the South Island from Lake Rotoiti in the north to Lake Hawea in the south (Bigelow, 1967). The specimens studied were, therefore, near the middle of the species range.

B. nivalis is abundant at Porter Heights above 4400 ft, and at Craigieburn above 4600 ft. The lower altitudinal limit of the species is determined by the lower limit of the screes. Specimens were collected from the top of Mt. Hamilton, which at 6290 ft was the highest point in the Craigieburn study areas.

1.4.d Paprides nitidus Hutton

Paprides nitidus is the smallest species studied. When alive it is easily distinguished from the other species by its

yellow coloured thoracic and abdominal sterna. This species shows geographical variation in notch-width of the female sub-genital plate (Bigelow, 1967; Peterson, 1968). The range of Paprides nitidus extends from Fox's Peak in South Canterbury to the Boulder Lakes area of northwest Nelson (Bigelow, 1967).

As stated in Table 1.4.2 Paprides nitidus is confined to vegetated areas. In general this means that in Canterbury the species would not extend to very high altitudes. At Porter Heights the species is found from about 3500 ft to the upper limit of the vegetation. At Craigieburn the lower limit of the species is at the bush edge. At Temple Basin P. nitidus has not been collected below 4300 ft and apart from one site between 4400 and 4700 ft is not at all abundant in the area. It is felt that the nature of the vegetation (which possibly represents a microclimatic preference) is important in the distribution of P. nitidus. The site where it is abundant at Temple Basin contains relatively tall tussocks and resembles the vegetated areas at Craigieburn and Porter Heights.

At Craigieburn both Paprides nitidus and Sigaus australis (Section 1.4.e) were found in tussock islands at 5900 ft, at least 500 ft in altitude above the nearest vegetated area. This observation supports the view that the upper altitudinal limit for these two species, in the areas studied, is determined by the upper altitudinal limit of the vegetated areas.

1.4.e *Sigaus australis* (Hutton)

Sigaus australis is a large grasshopper. All specimens examined were characterized by the presence of a pale band at the anterior edge of the lateral lobe of the pronotum. This band, although clearly distinguishable on fresh material, was often barely recognizable on preserved material. *Sigaus australis*, like *Brachaspis collinus*, displays colour polymorphism; but, in *S. australis* it is limited to the ground colour, which can range from bright green through to purplish-black.

Sigaus australis ranges from Haast Pass in the south of the South Island to the south side of the Waimakariri River in Canterbury (Bigelow, 1967). Thus, at Craigieburn and Porter Heights the species is at the northern limit of its range.

This species lives in tussock areas, and its upper altitudinal limit appears to be determined by the upper limit of the tussock (see last paragraph of Section 1.4.d). At Porter Heights *S. australis* could be collected from about 3500 ft to the extent of the tussock; while at Craigieburn its lower altitudinal limit was at the treeline.

1.4.f *Sigaus villosus* (Salmon)

Sigaus villosus is the largest grasshopper studied. This species lives on screes, and was never collected below 5000 ft. None of the specimens examined showed any sign of stripes. Like

Brachaspis nivalis, this species is grey, but it can be distinguished from B. nivalis by its size and its black eyes.

Because of its restriction to high altitudes the distribution of S. villosus is not well known. Available information (Bigelow, 1967) would suggest that the study areas were near the middle of its range.

1.5 Zonation

The system of altitudinal zonation adopted by Hayward (1967) for the Waimakariri catchment is as follows:

below 1000 ft	Lowland
1000 - 3000 ft	Montane
3000 - 4500 ft	Upper montane grassland
	OR
3000 - 4500 ft	Subalpine scrub
above 4500 ft	Alpine

Using this system the grasshoppers (Section 1.4) occupy the upper montane (subalpine) and alpine zones. But as they do not, in most cases, become abundant till about 4500 ft, they can be considered as truly alpine animals. The lower margin of the alpine area corresponds approximately to the treeline and to the lower limit of permanent winter snow.

1.6 Additional Material

Grasshoppers from sites other than the three study areas were occasionally collected by the writer, or given by their collector to the writer. The location and altitude of each collection site and a list of the species present in each collection is summarized in Table 1.6.1. The location of each site is shown in Fig 1.2.1.

Table 1.6.1: Additional material.

Collection Site	Species in collection	Altitude (ft)
Porters Pass	Brachaspis nivalis Paprides nitidus Sigaus australis	3000-4000
Amuri Ski Field	Brachaspis collinus Paprides nitidus	4900
Donald Hill, Glenariffe Station	Paprides nitidus Sigaus australis	4000-5000
Saddle between Lake Clearwater and Rangitata River	Paprides nitidus Sigaus australis	3500-4000
Crawford Range	Paprides nitidus	5000
Jellicoe Ridge	Brachaspis collinus Sigaus villosus	6500
Mt. Bruce, Bealey	Paprides nitidus	3500
Mt. Aicken	Brachaspis collinus	6000

Because the number of specimens in each collection was small, only a limited amount of information could be obtained from them. None of the collections extend the ranges of their component species, but several are from sites for which no records are available.

1.7 Collecting Techniques

In response to a disturbance grasshoppers react in one of three ways: (a) they do not move at all, (b) they retreat between the stones on a scree or into the plants in a vegetated area, or (c) they leap into the air. Response (c) was more common, particularly during hot weather. The grasshoppers were captured using insect nets either to trap them on the ground or net them in mid air. Smaller grasshoppers could be collected most satisfactorily by sweep netting, but larger individuals had to be pursued individually.

When handled, the grasshoppers often regurgitated a reddish-brown fluid and frequently tried to bite the hand of the collector. Mr. J. Illingworth (Marine Department, Wellington, pers. comm.) claims that a specimen of Brachaspis collinus managed to pierce his skin and draw blood. The biting was in response to being handled. There are no records of New Zealand alpine grasshoppers approaching humans and attempting to bite them.

Gangwere (1966) found that very few species of Catantopinae (the group to which Bigelow, 1967, has tentatively assigned the New Zealand alpine grasshoppers) tried to nip under any conditions.

Grasshoppers were difficult to capture early in the morning as they were sluggish and consequently difficult to detect. Similarly, during cold weather, when it was raining or snowing, or when there was a strong wind, collection was difficult if not impossible. Ideal collecting weather was warm to hot with very little wind. Under these conditions the grasshoppers were very active and easy to catch.

Captured grasshoppers were put into plastic bags and stored in these until sorted in the laboratory. It was found that if the number of specimens per bag was kept reasonably low the grasshoppers did not appear to suffer any ill effects if kept in this manner for two to three days.

At the laboratory the grasshoppers were anaesthetized with carbon dioxide and sorted. Specimens were caged (see Section 2.1); or killed, fixed and stored in arthropod fixative (70% alcohol - 20 parts, glacial acetic acid - 1 part, glycerine - 1 part). Ether was tested as an anaesthetic, but although it anaesthetized the animals for a longer period of time, it was rejected because the insects did not appear to live as long after revival as animals anaesthetized with carbon dioxide.

The animals killed on return to the laboratory will subsequently be called field grasshoppers, while those kept in cages

in the laboratory will be called laboratory grasshoppers.

Laboratory grasshoppers were removed from their cages when they died, and were then fixed and preserved in arthropod fixative.

1.8 Mensuration and Analysis of Numerical Data

Most morphological measurements used in this study were made using one of three sets of apparatus:

A - eyepiece micrometer in an Olympus Model E compound microscope.

B - eyepiece micrometer in an Olympus Model X stereoscopic microscope.

C - Vernier calipers.

The choice of apparatus depended on the size of the object being measured. Table 1.8.1 shows the size range measured by each set of apparatus and the possible error of the measurement.

Table 1.8.1: Error in Measurements.

Size Range of Measurement	Error	% Error	Apparatus*
< 1 mm	$\pm$ 0.010 mm	$< \pm$ 1.7	A
1-2 mm	$\pm$ 0.015 mm	$< \pm$ 1.1	B
2-10 mm	$\pm$ 0.025 mm	$< \pm$ 1.25	B
10-16.3 mm	$\pm$ 0.04 mm	$< \pm$ 0.4	B
> 16.3 mm	$\pm$ 0.05 mm	$< \pm$ 0.3	C

* For explanation of letters see text.

Unless otherwise stated, all biological measurements were made using the apparatus appropriate for the size range being measured.

Samples of five or more measurements were processed by the University of Canterbury I.B.M. 360/44 computer (128K bytes capacity), using Zoology Program A1. This program calculates and prints out the following statistics: mean*, median*, variance, standard deviation, coefficient of variation*, measure of skewness g_1*, measure of kurtosis g_2* and the maximum deviation of the data from a normal frequency distribution as calculated by the Kolmogorov-Smirnov Test, and prints the standard error and 99 or 95% confidence limits of the statistics identified by an asterisk. None of the data analysed differed significantly from a normal frequency distribution.

Section 2

REARING AND BEHAVIOUR OF GRASSHOPPERS

2.1 Maintaining Grasshoppers in the Laboratory

Attempts were made to rear the grasshoppers in cages in the laboratory and outdoors at Christchurch (altitude about 50 ft).

In the laboratory grasshoppers were kept in cages as shown in Fig 2.1.1. The bottom was removed from a 20 cm diameter tinned steel biscuit tin, and replaced with copper gauze of a suitable mesh. A 30 cm high tube was constructed from acetate sheet such that it fitted firmly when pushed on to the biscuit tin. The lid of the biscuit tin with its top removed, and a nylon stocking stretched over it for use as a handling sleeve, was placed on top of the tube. This type of cage is similar to that described by Hunter-Jones (1966). These cages were found, after experimentation with other types of cage, to be the easiest to use and keep clean, and most suitable for the grasshoppers. Caged animals were provided with distilled water in cotton-wool plugged vials and regularly fed fresh dandelion leaves (Taraxacum officinale). Cages containing adults were provided with small plastic pots (5 cm in diameter, 3.5 cm deep) filled with damp sand for oviposition. The perching branches recommended by Hunter-Jones (1966) were unecessary, because the grasshoppers could easily climb the vertical acetate sheet.

Outdoors the grasshoppers were kept in cubical cages of 1 m side constructed from wood and terylene netting with an external protective layer of wire netting. This cage was placed over a

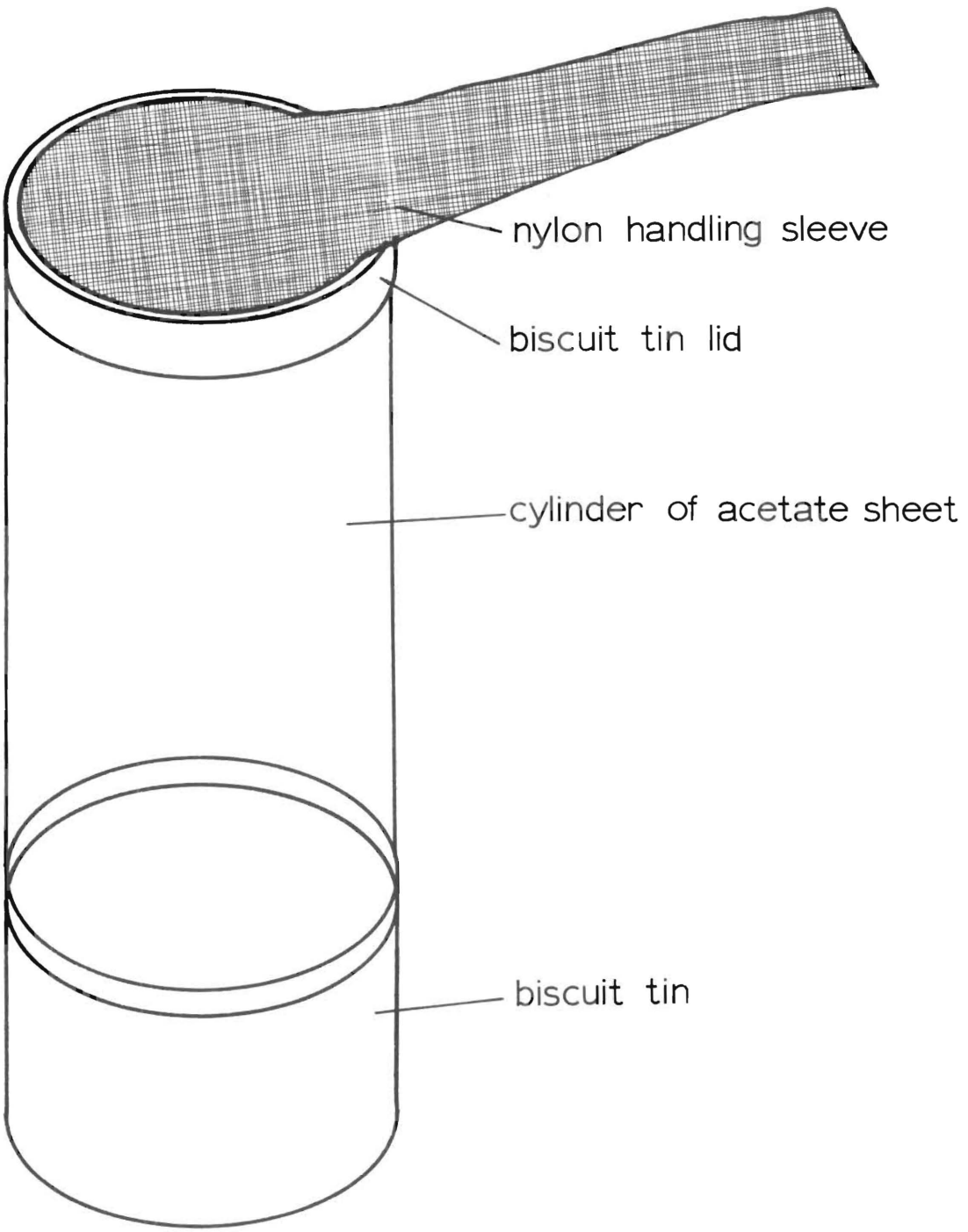

nylon handling sleeve
biscuit tin lid
cylinder of acetate sheet
biscuit tin

Figure 2.1.1

Diagram of grasshopper cage.

variety of possible food plants, which had not been sprayed in recent memory. Grasshoppers of various species and instars were introduced. The number of grasshoppers was kept low to avoid high density effects. The first grasshoppers introduced died within two months. The cage was then moved to another site and newly collected grasshoppers were introduced on two occasions, but with similar results.

Grasshoppers caged in the laboratory appeared to remain healthy for approximately three weeks, after which they became sluggish, lost weight and slowly died. Most moults and ovipositions that occurred in the laboratory took place during this three week period. Few juveniles passed through more than one moult in the laboratory. Occasional animals and occasional cages did not conform to this pattern and remained apparently healthy for a longer period of time. Cage design, food plants, air temperature, light regime and grasshopper density were all modified in an attempt to maintain the grasshoppers for a longer period of time, but with no success. It was observed that shifting the grasshoppers to a higher temperature appeared to revitalize the culture temporarily. This could have been due to increased metabolic rate at the higher temperature, and may have had no long term significance.

The grasshoppers caged outdoors remained apparently healthy for a longer period of time than those caged in the laboratory. But results indicated that the environment outdoors was also

unsuitable for the grasshoppers. Observation of the grasshoppers while alive, and careful examination of the cage site after the death of all the grasshoppers suggested that none of the caged juveniles had moulted and that none of the caged adult females had oviposited. They had all, however, died within two months of being collected from the field.

2.2 Courting and Copulation

Observations showed that the grasshoppers have a courting ritual. The extent and nature of this ritual was variable. In the most extended form, the male approached the female flicking his hind legs (exposing the red colour on their internal faces). The female either ignored these approaches, in which case the male transferred his attentions to another female or stopped the behaviour; or, she turned to face the approaching male and flicked her hind legs. In the latter case, the male and female would face each other and intersperse flicking of hind legs with touching of antennae, until the male mounted the female. Once mounted he manoeuvered his abdomen into position with one hind leg. When correct position was achieved the everted genitalia of the male interlocked with the genitalia of the female. Other males were observed to mount females without going through any observable courtship ritual. All species appeared to have a

similar courtship ritual.

Fig 2.2.1 shows a pair of Brachaspis nivalis adults copulating. A similar position was adopted by the other species during copulation. It was observed that the abdomen of the male could be curled around either side of the abdomen of the female. Grasshoppers remained in copulo for considerable lengths of time. Two pairs of Brachaspis collinus separated in response to a disturbance after being interlocked for 27 hours.

Grasshoppers were frequently observed in copulo in the field. They showed little hesitation about mating, either when collected or in the laboratory, which suggests that copulation probably occurs several times.

The patterns of courtship and copulation exhibited by the New Zealand alpine grasshoppers are similar to those exhibited by other acridids (Uvarov 1928 and 1966a). The New Zealand alpine grasshoppers, because of the small size of their tegmina, cannot stridulate.

2.3 Oviposition

The New Zealand alpine grasshoppers, like most acridids, lay their eggs in batches. The eggs in a batch are held together and enveloped by a frothy substance which is secreted while the eggs are being laid. The eggs plus secretions constitute an egg

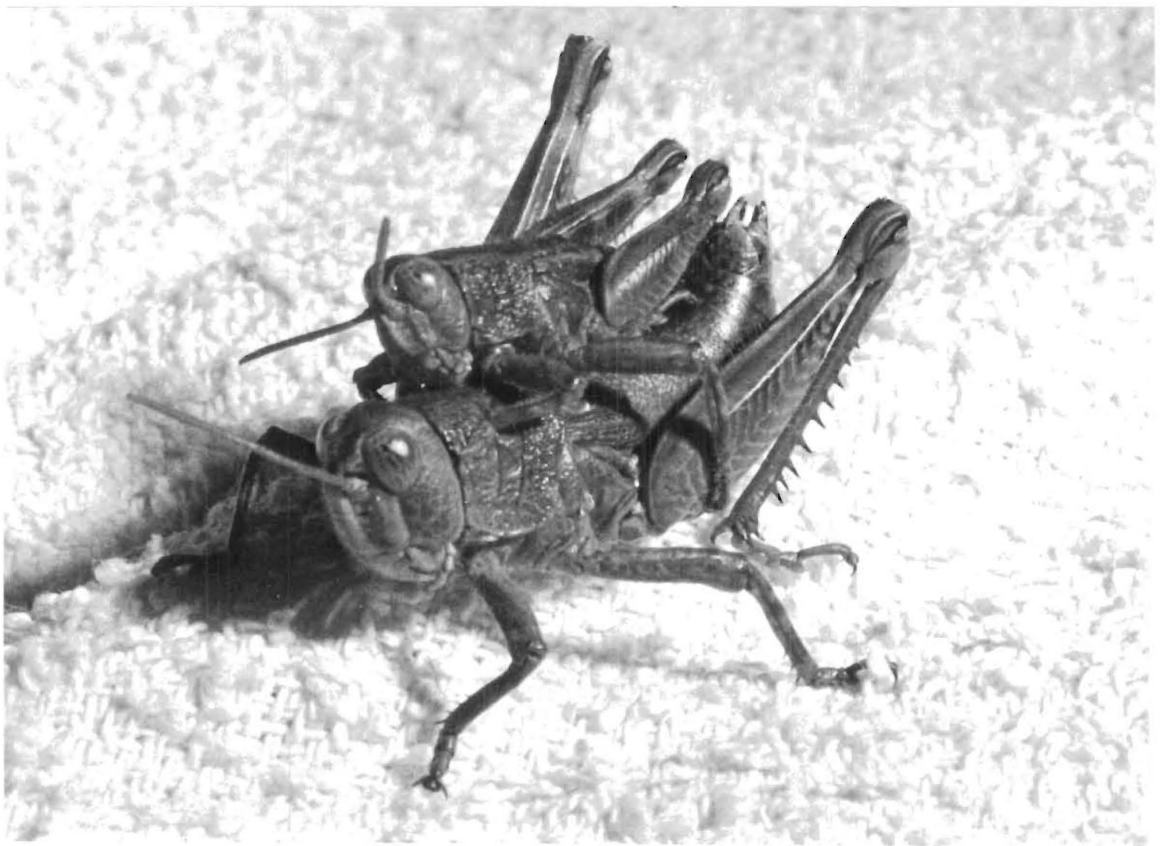


Figure 2.2.1

Copulating pair of *Brachaspis nivalis*.

pod. The number of eggs per pod, and the arrangement of eggs in a pod, varied with species. Egg pod structure and the characteristics of specific egg pods are described in Section 3.7.

No grasshoppers were observed ovipositing in the field. Some eggs were, however, collected in the field. All these were found just below the surface of the soil, in small, vegetation-free terraces. Eggs were discovered by digging the soil in these terraces, but successful discoveries of eggs were very rare.

All caged grasshoppers were provided with sand dishes (Section 2.1) for oviposition. Fig 2.3.1 shows a grasshopper ovipositing in one of these dishes. Oviposition was only infrequently observed in the laboratory as it usually occurred at night. The subject of Fig 2.3.1 was found on return to the laboratory at night. She was disturbed by the photography and did not complete her pod, but even so, she rested for 30 minutes after retraction of her abdomen before leaving the oviposition site.

Egg pods were usually deposited 0.5 - 1 cm below the surface of the sand, and the angle of the pod was anywhere between perpendicular and parallel to the sand surface. The grasshoppers made no effort to fill or disguise the hole made during oviposition.

Damp sand was preferred over dry sand, damp perlite, fine gravel or garden soil as an oviposition medium. Oviposition appeared to be accelerated by keeping the grasshoppers in the

Figure 2.3.1

Paprides nitidus adult female ovipositing.

dark at high temperatures.

A "loose clutch", as defined by Smith (1969), is a mass of froth, with eggs dispersed in a random manner through it, deposited on the walls or floor of the cage. On several occasions loose clutches were noted in the laboratory cages. Smith (1969), in his work on Melanoplus sanguinipes, observed that virgin females laid loose clutches when caged individually and normal pods when in crowded cages. The loose clutches noted in this study were laid by females in cages containing several other grasshoppers.

Five Brachaspis collinus sixth instar females were collected in the field and caged at 39°C. Only one female moulted to the adult stage and 24 days after moulting this female laid a loose clutch of eggs. Because she had had no contact with male grasshoppers since becoming an adult, she must have been a virgin. Other loose clutches, however, were laid by adult females in circumstances where they would not be expected to be virgins.

2.4 Rearing Nymphs from Eggs that Hatched in the Laboratory

Grasshopper eggs were kept on damp sand in petri dishes. Most eggs were laid by adult female laboratory grasshoppers, but a few were collected in the field. Very few of the eggs kept in the laboratory hatched, but when they did attempts were made

to rear the nymphs. When grasshopper eggs hatch they produce a "vermiform" larva which quickly goes through the so-called intermediate moult to become a first instar. Attempts were made to rear only grasshoppers which had completed their intermediate moult. The eggs of all the grasshopper species studied go into an obligatory diapause which could not be broken predictably (Section 4.6); therefore, eggs did not hatch frequently and newly hatched grasshoppers were not abundant.

The results of attempts to rear nymphs from eggs that hatched in the laboratory are shown in Table 2.4.1. Only grasshoppers which had passed through their intermediate moult were caged, but all died before moulting to second instar. No nymphs lived for longer than 18 days.

The reasons for the death of the newly hatched grasshoppers is unknown. The nymphs stayed on the floors of their cages. Those in cages five and seven lived for seven and nine days respectively before they started dying, but those in the other cages started dying within one to four days of hatching. Cages five and seven had damp perlite floors and therefore would have been more humid than the other cages. High humidity may be necessary for the nymphs. The newly hatched grasshoppers were removed from the egg dishes to cages using an aspirator. It was suggested by Dr. Kevan of Macdonald College, Canada, that this may have damaged the hoppers. Lack of newly hatched grasshoppers prevented further experiments using high humidities

Table 2.4.1: Cage records for grasshoppers hatched in the laboratory.

Cage No.	Source of eggs	Species	Cage type	Temperature (°C)	Hopper life (days)	N
1	Field	*Brachaspis collinus*	Plastic canister 9x9x12 cm with perforated top	R*	3-13	8
2	"	"	"	R	3-9	18
3	Lab.	"	20x20x20 cm, wooden frame, floor & back, gauze sides & front, plastic top	R	4-18	21
4	"	"	Grasshopper cage (see Section 2.1)	R	4	7
5	"	"	As cage 3, but gauze floor and placed over damp perlite	R	7	4
6	"	*B. nivalis*	As cage 3	R	1-10	16
7	"	"	As cage 5	28	9-18	7
8	Field	*Sigaus australis*	As cage 3	38	1-2	12
9	"	"	As cage 3	30	1-3	12

* R = room temperature = 20 ± 5°C

N = number of first instar grasshoppers caged

and animals not handled by aspirator.

2.5 Discussion

Grasshoppers collected in the field could not be reared either in cages in the laboratory or in outdoor cages just above sea level. They could, however, be maintained in these cages for variable lengths of time. Similarly, no method was discovered for rearing grasshoppers from eggs that hatched in the laboratory, nor for maintaining these grasshoppers.

The New Zealand alpine grasshoppers obviously live successfully in their alpine environment. Their inability, however, to live successfully at low altitudes suggests that they are intimately bound to the alpine environment. Because it was not possible to maintain any of the stages (except the egg) for any length of time in the laboratory, it would appear that this restriction is probably physiological. Their behaviour under lowland conditions, therefore, although normal for these conditions, would be abnormal in their natural environment and therefore bears little relation to their normal behaviour in the field.

Section 3

MORPHOLOGY, ANATOMY AND EGG POD STRUCTURE

3.1 Introduction

Aspects of the external morphology of New Zealand alpine grasshoppers have been described and/or measured by each of the following authors: Bigelow (1967), Batcheler (1967), Hudson (1967 and 1970), Staples (1967), Green (1967) and Peterson (1968). There is, however, no published information on either the internal anatomy of these animals or their egg pod structure. The data presented in this section include an estimate of the variation in each measured character. Comparisons have been made between species and between populations of the same species from different areas. These comparisons are summarised in Section 3.8. Egg pod structure is included in this section because it provides an additional means of comparison between species.

Bigelow (1967) and Staples (1967) showed that grasshoppers increased in size with increasing altitude. Because of this, collecting was usually confined to the altitudinal range 4500 to 5500 ft. Sigaus villosus, because it is confined to very high altitudes, was collected only between 5000 and 6000 ft.

3.2 Pronotum and Femur Length

Hind femur length, and the length of the median carina of

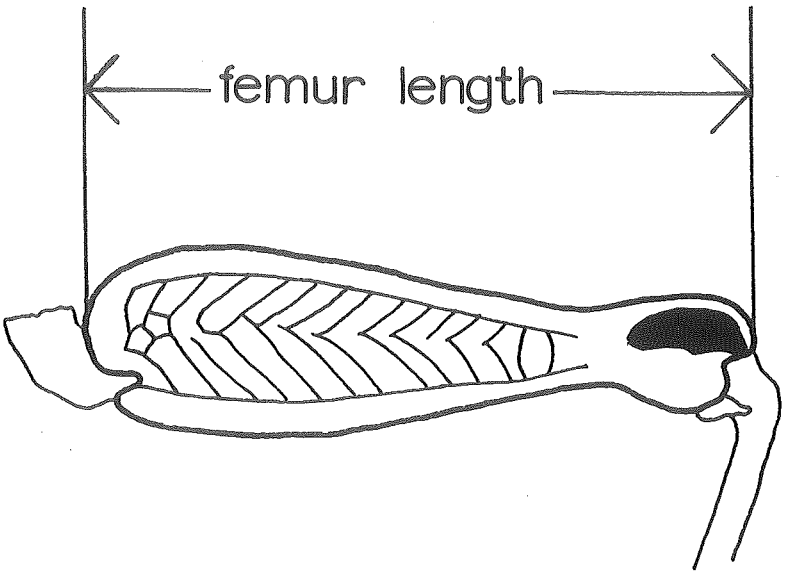
the pronotum, were measured as shown in Fig 3.2.1. These characters were chosen because they are easily measured, because they provide an estimate of size variation in separate populations, and because their size facilitates the identification of instars. Both characters are very precisely defined, and thus the measurements of different workers can be compared directly.

The measurements made during this study are compared with those recorded by Bigelow (1967), Hudson (1970) and Staples (1967). Bigelow (1967) described the external morphology of the adult New Zealand grasshoppers, and where data were available discussed specific geographical and altitudinal size variation. The external morphology of the juvenile alpine grasshoppers was described by Hudson (1970) who listed the femur lengths of the specimens she examined in an appendix. Staples (1967) examined altitudinal size variation in Brachaspis collinus at Temple Basin and listed femur length and width, and pronotum length of the specimens he examined in an appendix.

Most measurements were taken from specimens preserved in arthropod fixative. Comparisons of fresh with preserved specimens showed that this preservation had no significant effect on either femur or pronotum length (see Table 3.2.1). Comparisons of right and left femora showed that the right femora did not differ significantly from the left femora in the populations as a whole.

Figure 3.2.1

Location of femur length and pronotum length measurements.


femur length

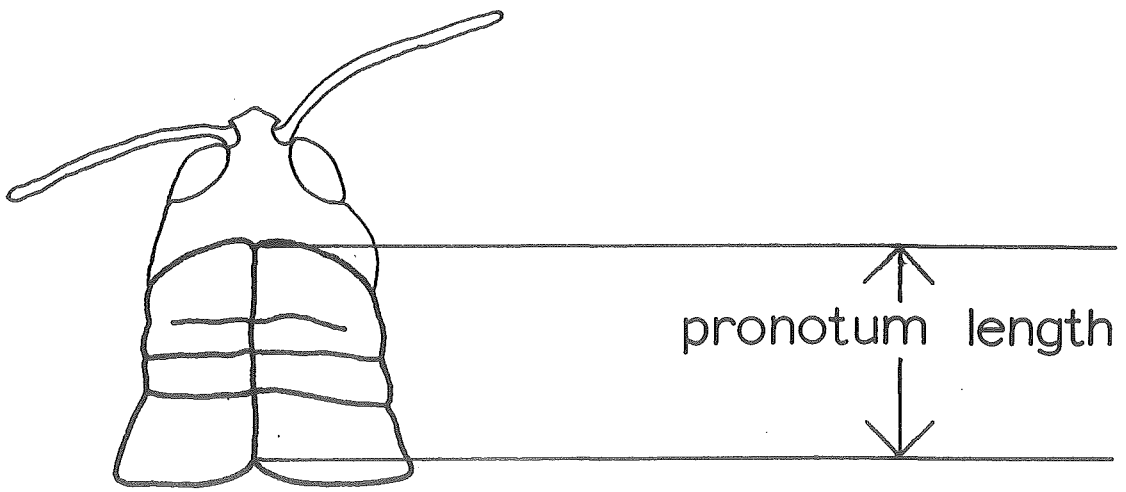

pronotum length

Table 3.2.1: Comparison of left and right femur lengths and femur and pronotum lengths of fresh and preserved (in arthropod fixative) adult specimens of Brachaspis collinus.

	Mean (mm)	S	N	t	P
Adult male femur length					
fresh	14.10833	0.43788	12	0	1.00
preserved	14.10833	0.54807	12		
Adult male pronotum length					
fresh	4.66249	0.27742	8	1.672956	.1 < p < .2
preserved	4.87749	0.23487	8		
Adult male femur length					
left	13.91526	0.58917	19	0.024267	p > .5
right	13.91999	0.51859	19		
Adult female femur length					
left	18.63884	0.53483	18	0.029888	p > .5
right	18.64441	0.58231	18		

S = Standard deviation

N = number in sample

t = value of Students "t"

P = probability of obtaining t

Measurements were not taken from animals which had moulted in the laboratory. Available data were insufficient to determine if there was any significant size difference between animals which had moulted in the laboratory and those which had not.

The measurements of femur and pronotum length made during this study are summarized in Table 3.2.2. Although only the mean of each sample is shown in the table, the mean, 99% confidence limits of the mean, coefficient of variation, value of D-max by the Kolmogorov-Smirnov Test, and the number in each sample, are tabulated in Appendix Tables I-XIV. Separate analyses are included of specimens from each local population.

Brachaspis collinus does not occur at Craigieburn or Porter Heights and was taken only at the Temple Basin study area. Staples (1967) found that this species, in the same study area, increased in size with altitude. Measurements made in this study lie within the range found by Staples, and do not differ significantly in femur length (by "t" tests) from the adults in the "Arthurs Pass" group of Bigelow (1967). Femur lengths of juveniles are of the same order as those recorded by Hudson (1970) except for instar VI males which are significantly larger than Hudson's "Arthurs Pass" specimens (probability less than 0.05 by "t" test).

Brachaspis nivalis is present at the Craigieburn and Porter Heights study areas. The femur and pronotum lengths of male and female adults from the two study areas are compared in

Table 3.2.2: Mean femur and pronotum lengths of collected grasshoppers. (All measurements in millimetres.)

Sex	Instar	Species: Brachaspis collinus	Brachaspis nivalis	Paprides nitidus	Sigaus australis	Sigaus villosus
Femur Length						
Male	adult	14.39	11.07	10.48	11.42	15.81
	VI	12.18	9.87	8.86	9.32	13.75*
	V	9.73	7.97	7.31	7.71*	11.08*
	IV	7.83	6.39	5.79	N.A.	8.48*
	IIIA	6.27	5.23	-	-	6.70*
	II	4.71	4.39*	4.30	4.13*	5.43
	I	3.58	3.15*	3.30*	3.27	N.A.
Female	adult	18.62	14.80	15.15	17.97	20.86
	VI	15.40	12.30	12.08	14.12	16.55*
	V	12.35	12.12	9.60	10.93	14.35*
	IV	9.94	8.64	7.52	8.38	12.20*
	IIIB	7.86	6.68	5.80	6.48	N.A.
	IIIA	6.15	5.68	-	-	6.85*
	II	4.78	4.35*	4.49	4.33*	1.43*
	I	3.57	3.07*	N.A.	3.18*	N.A.
Pronotum Length						
Male	adult	4.83	3.70	3.67	3.42	5.34
	VI	4.44	3.43	3.25	3.07	4.92*
	V	3.55	2.87	2.75	2.71*	4.17*
	IV	2.81	2.33	2.00	N.A.	3.03*
	IIIA	2.19	1.84	-	-	2.40*
	II	1.58	1.46*	1.48	N.A.	1.77
	I	1.14	1.12*	0.99*	1.10*	N.A.
Female	adult	6.43	4.96	5.18	5.49	7.27
	VI	5.55	4.32	4.24	4.58	6.38*
	V	4.48	3.59	3.38	3.67	5.12*
	IV	3.55	3.13	2.61	2.84	4.30*
	IIIB	2.75	2.36	1.99	2.15*	N.A.
	IIIA	2.12	1.96	-	-	2.28*
	II	1.60	1.69*	1.45	1.43*	N.A.
	I	2.21	1.28*	N.A.	1.053*	N.A.

N.B. Mean, 99% confidence limits of mean, standard deviation, coefficient of variation, value of D-max by Kolmogorov-Smirnov Test and sample size for each of the above samples are shown in Appendix Tables I, IV, VIII, XI, XIV.

N.A. = no data available: * = sample contained less than five measurements: - = this instar is absent in the species concerned.

Table 3.2.3. It will be noted that femur and pronotum length in both sexes are significantly longer in the Craigieburn population (probability by "t" tests less than 0.005). Bigelow (1967) considered there was a clinal size increase in adults of this species and stated that body size increased with altitude. Craigieburn adults measured in this study do not differ significantly in femur length (by "t" tests) from Bigelow's "Craigieburn" adults. The Porter Heights specimens measured in this study were, however, found by "t" tests to be significantly smaller in femur length than Bigelow's "Craigieburn" specimens (probability less than 0.001 in both males and females) and "Torlesse" specimens (probability less than 0.05 in males and less than 0.001 in females).

This study contains the first record for Brachaspis nivalis of instar IIIB females and instar I males and females. These instars were assumed to exist by Hudson (1970) but had not been examined by her. As only a few juveniles of Brachaspis nivalis were examined by Hudson (1970), these measurements provide useful additional data.

Paprides nitidus was the only species which occurred in each of the three study areas. Pronotum and femur lengths of adults from each population are compared in Tables 3.2.4 and 3.2.5. "t" tests show that the adult males from Temple Basin differ significantly in femur and pronotum lengths from the adult males from Craigieburn and Porter Heights (probability less than

Table 3.2.3: Comparison of femur and pronotum lengths of adult *Brachaspis nivalis* from Craigieburn and Porter Heights study areas.

	Mean (mm)	S	N	t	P
Male femur length					
Craigieburn	11.52894	0.66902	19	6.041407	$p < .001$
Porter Heights	10.72910	0.60087	35		
Male pronotum length					
Craigieburn	3.80750	0.23425	20	3.066965	$.005 > p > .001$
Porter Heights	3.63913	0.17066	35		
Female femur length					
Craigieburn	15.26466	0.71250	34	4.274239	$p < .001$
Porter Heights	14.60760	0.71764	60		
Female pronotum length					
Craigieburn	5.10222	0.27340	36	3.624275	$p < .001$
Porter Heights	4.90429	0.25692	65		

S = standard deviation

N = number in sample

t = value of Students "t"

P = probability of this value of t occurring by chance

Table 3.2.4: Comparison of femur and pronotum lengths of adult *Paprides nitidus* from each study area.

	Mean (mm)	S	N
Male femur length			
Craigieburn	10.32199	0.53296	15
Porter Heights	10.40677	0.53647	44
Temple Basin	10.63734	0.28533	54
Male pronotum length			
Craigieburn	3.58499	0.22719	16
Porter Heights	3.65045	0.12616	44
Temple Basin	3.73092	0.19023	54
Female femur length			
Craigieburn	15.19687	1.26243	16
Porter Heights	15.26206	0.65072	61
Temple Basin	15.18073	0.52326	111
Female pronotum lengths			
Craigieburn	5.13444	0.35261	18
Porter Heights	5.23950	0.25584	62
Temple Basin	5.19029	0.19983	113

S = standard deviation

N = number in sample

Table 3.2.5: Analysis of measurements of Paprides nitidus in Table 3.2.4.

Character	Populations Compared		
	Porter Heights & Craigieburn	Craigieburn & Temple Basin	Porter Heights & Temple Basin
Male femur lengths			
"t"	0.529408	2.729359	3.071335
probability	$p > .5$	$.01 > p > .005$	$.005 > p > .001$
Male pronotum lengths			
"t"	1.413899	2.576653	2.406622
probability	$.2 > p > .1$	$.025 > p > .01$	$.025 > p > .01$
Female femur lengths			
"t"	0.286229	0.091808	0.892886
probability	$p > .5$	$p > .5$	$.4 > p > .2$
Female pronotum lengths			
"t"	1.402999	1.409356	1.013446
probability	$.2 > p > .1$	$.2 > p > .1$	$.4 > p > .2$

"t" = Students "t"

0.01 for femur length and less than 0.05 for pronotum length). No comparable differences exist between the adult females. Comparison (using "t" tests) with adult femur lengths recorded by Bigelow (1967) shows that the Craigieburn females do not differ significantly from Bigelow's "Craigieburn" females, the Craigieburn and Porter Heights males do not differ significantly from Bigelow's "Torlesse-Craigieburn" males, the Temple Basin females do not differ significantly from Bigelow's "Arthurs Pass" females, but that the Temple Basin males are significantly larger than Bigelow's "Binser-Arthurs Pass" males (probability less than 0.001). Four instar I males were examined during this study, this instar was not found by Hudson (1970) but she assumed it did occur. The juvenile specimens of Paprides nitidus were similar in femur length to the "Fog Peak" and "Craigieburn River" specimens measured by Hudson (1970).

Sigaus australis was collected from Craigieburn and Porter Heights study areas. A comparison of femur and pronotum lengths of Craigieburn and Porter Heights adults using "t" tests (Table 3.2.6) shows that these two populations do not differ significantly in these characters. Bigelow (1967) noted that Sigaus australis showed geographical and altitudinal variation in size, he did not, however, examine any specimens from the Craigieburn Range. The measurements made during this study show that specimens from the Craigieburn Range are intermediate in femur length between Bigelow's "Fox's Peak" and "Torlesse" populations,

Table 3.2.6: Comparison of femur and pronotum length of adult *Sigaus australis* from Craigieburn and Porter Heights study areas.

	Mean (mm)	S	N	t	P
Male femur length					
Craigieburn	11.3500	0.2858	4	0.02064	$p > .5$
Porter Heights	11.42812	0.73046	16		
Male pronotum length					
Craigieburn	3.395	0.1578	4	0.28873	$p > .5$
Porter Heights	3.4222	0.17261	18		
Female femur length					
Craigieburn	17.93999	1.03586	5	0.165140	$p > .5$
Porter Heights	17.99223	0.66249	78		
Female pronotum length					
Craigieburn	5.57833	0.22982	6	0.27230	$p > .5$
Porter Heights	5.49154	0.24915	82		

S = standard deviation

N = number in sample

t = value of Students "t"

P = probability of value of t

and thus support the clinal variation in size found by Bigelow. This study contains the first record of Sigaus australis instar I males and females. These instars were assumed to exist by Hudson (1970) but were not found by her. The measurements of femur length made during this study and those recorded by Hudson (1970) suggest that the juveniles of Sigaus australis show the same clinal variation in size as Bigelow (1967) found for the adults.

Sigaus villosus was found at the Craigieburn and Porter Heights study areas. A comparison of these two populations, using "t" tests, shows that they do not differ significantly in femur and pronotum length (Table 3.2.7). Bigelow (1967) lumped samples of this species taken from his "Craigieburn", "Torlesse" and "Mt. Binser" areas into a single sample he called "Central". The adult females examined in this study from Craigieburn and Porter Heights did not differ significantly in femur length from Bigelow's "Central" adult females, but the adult males from both Craigieburn and Porter Heights were significantly smaller in femur length than the males of Bigelow's "Central" sample ("t" tests gave probability values of less than 0.025 and less than 0.001 respectively). This study contains the first record of an instar IIIA male and of instar II males of Sigaus villosus. As for the other species these instars were assumed to exist by Hudson (1970), but had not been found by her. Hudson (1970) did not examine a large number of juveniles of Sigaus villosus;

Table 3.2.7: Comparison of femur and pronotum lengths of adult Sigaus villosus from Craigieburn and Porter Heights study areas.

	Mean (mm)	S	N	t	P
Male femur length					
Craigieburn	15.94000	0.40373	5	0.843877	.5 > p > .4
Porter Heights	15.73888	0.43859	9		
Male pronotum length					
Craigieburn	5.39600	0.32370	5	0.691388	p = .5
Porter Heights	5.32250	0.12764	12		
Female femur length					
Craigieburn	21.31248	0.60104	8	2.307507	.05 > p > .025
Porter Heights	20.77301	0.57171	26		
Female pronotum length					
Craigieburn	7.39624	0.27203	8	1.361055	.2 > p > .1
Porter Heights	7.25285	0.26035	28		

S = standard deviation

N = number in sample

t = value of Students "t"

P = probability of value of t

therefore, the measurements recorded here, although themselves incomplete, will provide additional information on this species.

In all observations of moulting the grasshoppers passed through a series of instars proposed by Hudson (1970). Hudson (1970) found that hind femur length, if it was used in conjunction with anatomical observations, could be useful for the purpose of identification of instars within a species, but noted that its usefulness was limited by intra-specific variation in widely distributed species. The measurements of Brachaspis collinus from Temple Basin show that each of the male instars and each of the female instars can be separated on femur length, provided the individuals examined are within two standard deviations of the mean femur length for their instar. That is, 95% of the population can, after sexing, be placed in their correct instar on the basis of femur length. Pronotum length cannot, however, be used in the same manner. The instars of the other species examined cannot as yet be separated in this way.

Morphological measurements made during this study have been compared with those recorded by Bigelow (1967), Staples (1967) and Hudson (1970). Despite the availability of the data of these authors it was felt necessary to record the measurements of femur and pronotum length made during this study for the following reasons:

1. Bigelow (1967) and Hudson (1970) have both shown that the New Zealand alpine grasshoppers exhibit geographical variation in size.

The measurements made during this study provide additional data on this subject and support the patterns of variation proposed by Bigelow.

2. The femur length measurements, and in the absence of other parts of the body the pronotum length measurements, are useful for the identification of instars. In many cases these are the first records of the femur and pronotum lengths of juvenile alpine grasshoppers from the Porters Pass through to Arthurs Pass region of Canterbury. They are, therefore, important because geographical variation in size can limit the usefulness for instar determination of comparable measurements made on grasshoppers from other areas.

3. Hudson (1970) does not present a complete series of measurements of all instars of one species from one area. This is provided in this study by the data for Brachaspis collinus from Temple Basin.

4. Eight instars are recorded and measured which Hudson (1970) had assumed to exist, but had not examined.

5. Use is made of these measurements in making comparisons between species and between different populations of the same species.

3.3 Aberrant Specimens

Apart from the occasional animal with an irregular pigmentation pattern, only three morphologically aberrant specimens were found. Two of these were "miniature" Brachaspis collinus adult females. These two females were found on dissection to have ovulated, indicating that they were sexually mature. They differed from normal adult females of Brachaspis collinus in wing structure and body size. Their tegmina were much shorter than in normal females, and projected laterally from the body (Fig 3.3.1). A comparison of the femur and pronotum lengths of each "miniature" female with the mean values for these dimensions in normal adult females of the species is shown in Table 3.3.1. One of the "miniature" females was significantly smaller (probability less than 0.001 by "t" tests) in both dimensions, while the other was significantly smaller only in femur length (probability less than 0.001 for femur length and between 0.1 and 0.2 for pronotum length).

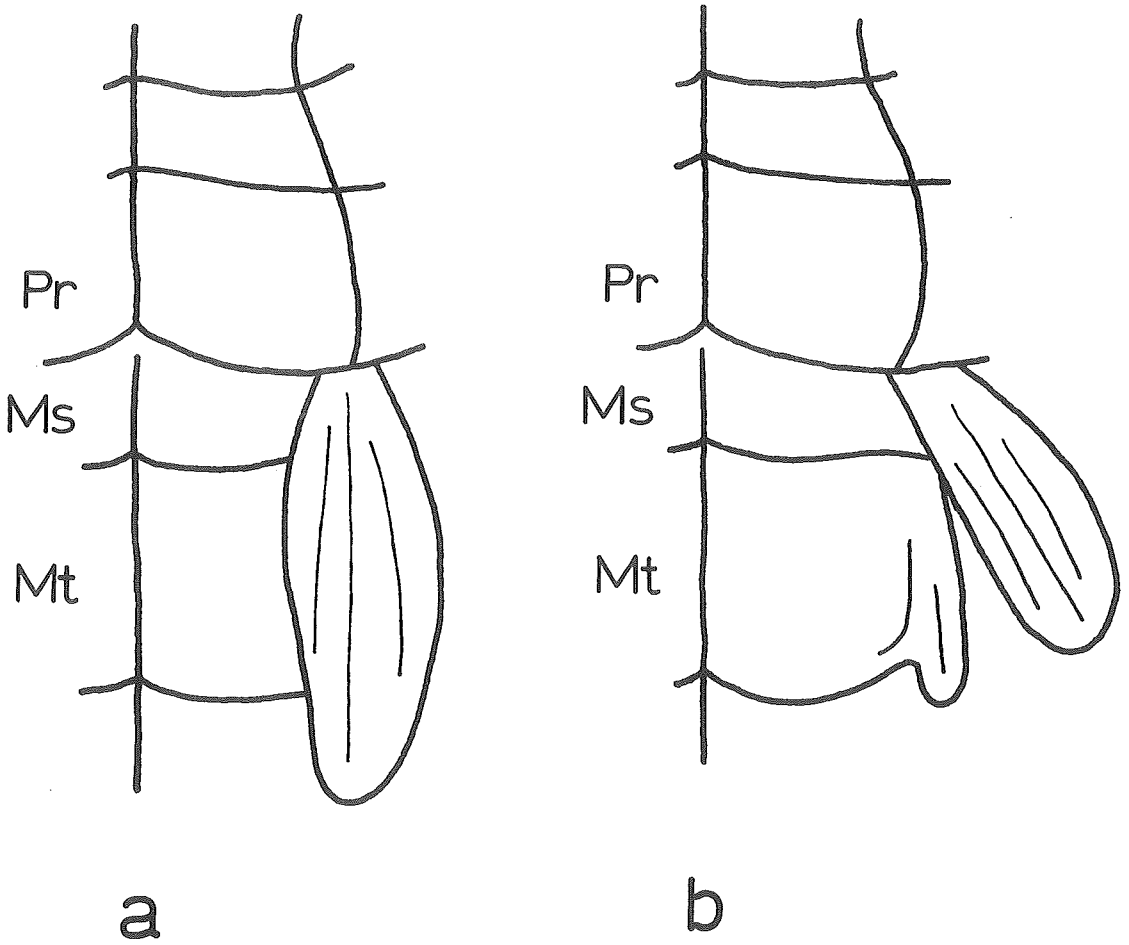
Both these Brachaspis collinus specimens were collected at Temple Basin in early 1967 and kept in cages in the laboratory. Neither moulted in the laboratory and neither contained parasites when examined. Their external genitalia, although smaller, appeared identical to those of normal adults.

An aberrant Paprides nitidus female was collected at Porter Heights in December, 1969. In wing structure it was intermediate

Table 3.3.1: Comparison of femur and pronotum lengths of "miniature" females with normal Brachaspis collinus adult females.

Character	"Miniature" female 1	Normal adult female	"Miniature" female 2
Femur length (mm)	13.4	18.6246	15.8
Standard deviation		0.66941	
Students "t"	7.804780		4.219537
Probability	$p < .001$		$p < .001$
Pronotum length (mm)	4.4	6.42874	6.0
Standard deviation		0.28307	
Students "t"	7.166920		1.514608
Probability	$p < .001$		$.1 < p < .2$

between the fourth and fifth instars. The wings were larger than those of fourth instar individuals but shorter than, and not reversed like those of a fifth instar specimen (Fig 3.3.2). The genitalia were slightly less developed than those of a typical fifth instar individual. Femur length (9.05 mm) and pronotum length (3.16 mm) did not differ significantly from the means for fifth instar females (probabilities were 0.2 - 0.4 and 0.1 - 0.2 respectively by "t" tests). General structure would suggest that this was a small Paprides nitidus fifth instar female in



a b

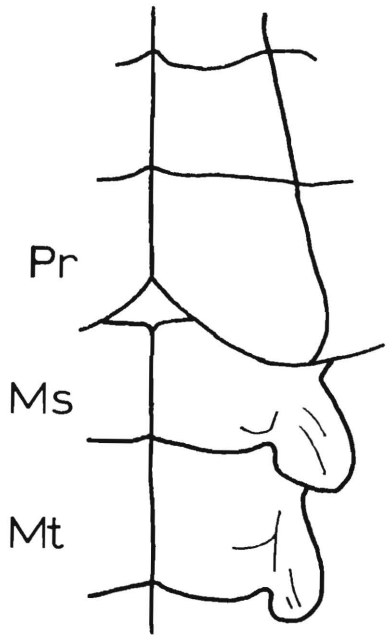
Figure 3.3.1

Dorsal view of wing structure of (a) normal adult female, and (b) "miniature" adult female of Brachaspis collinus.

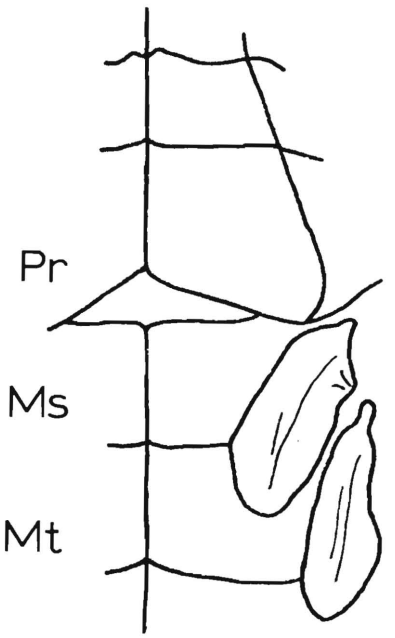
Pr = pronotum

Ms = mesonotum

Mt = metanotum



a



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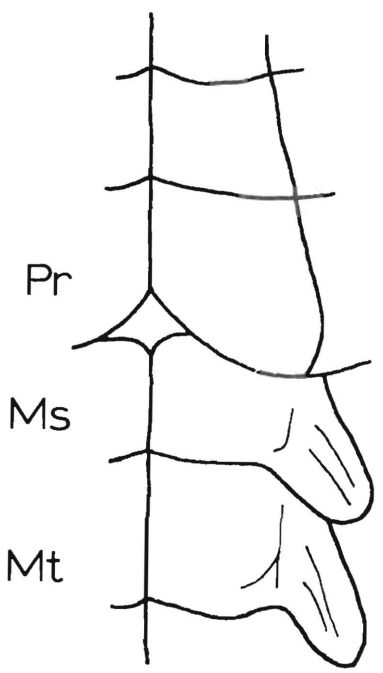


c

Figure 3.3.2

Dorsal views of the wing structures of female specimens of Paprides nitidus. (a) Fourth instar, (b) Fifth instar, (c) Aberrant specimen.

(a) and (b) are copied, with kind permission, from Hudson (1967).

Pr = pronotum

Ms = mesonotum

Mt = metanotum

which the wings had failed to reverse.

3.4 Alimentary Canal and Feeding

The alimentary canals of the five species studied follow the usual pattern for acridids (Uvarov, 1966a). Examination of the crop contents of a small sample of grasshoppers suggested that the major constituents of their diets were broad leafed plants, not grasses.

The feeding behaviour of New Zealand alpine grasshoppers in the Craigieburn Range has been studied by Watson (1971).

3.5 Male Gonads

In the species studied the male gonads were of the usual pattern for acridids (Uvarov, 1966a). The testes occupy the dorsal part of the abdominal cavity in adult males. In situ they appear to be a single structure, but are paired. Each testis is composed of a large number of follicles connected ventrally by thin tubes (vasa efferentia) to a vas deferens which runs to the posterior of the body and joins the ejaculatory duct. At the union of the ejaculatory duct and the vasa deferentia are a large number of blind tubes which constitute the male accessory

glands. These glands are also paired, and in the five species studied each set of accessory glands consisted of 16 tubes.

A diagrammatic lateral view of a single testis is shown in Fig 3.5.1. The follicles are connected to the vas deferens in a bilaterally symmetrical manner. Laird (1943) distinguished three major types of testis. The simplest was the "pinnate" in which follicles, usually very numerous, joined the seminal duct along the whole length of the testis. In the other extreme type, the "fountain", less numerous follicles entered the seminal duct near its blind end, in a cluster. The difference between these two types was not sharp, and a third "intermediate" type had to be recognized. All types can be found in the Catantopinae, to which group Bigelow (1967) has tentatively assigned the New Zealand alpine grasshoppers. Laird (1943) assigned a testis to a particular category using the ratio of vasa efferentia length to gonad length. Vasa efferentia length (V.E.L.) is the length of vas deferens from the blind end to the point where the most posterior vas efferens enters. Gonad length (G.L.) is the distance from the blind end of the vas deferens to the end of the most posterior follicle (see Fig 3.5.1). "Pinnate" testes have a V.E.L. to G.L. ratio greater than 0.5, "intermediate" about 0.5 and "fountain" less than 0.5.

Measurements of V.E.L., G.L. and follicle number were not easy to obtain. Grasshoppers were dissected from the dorsal surface and the testes had to be removed without damage, before

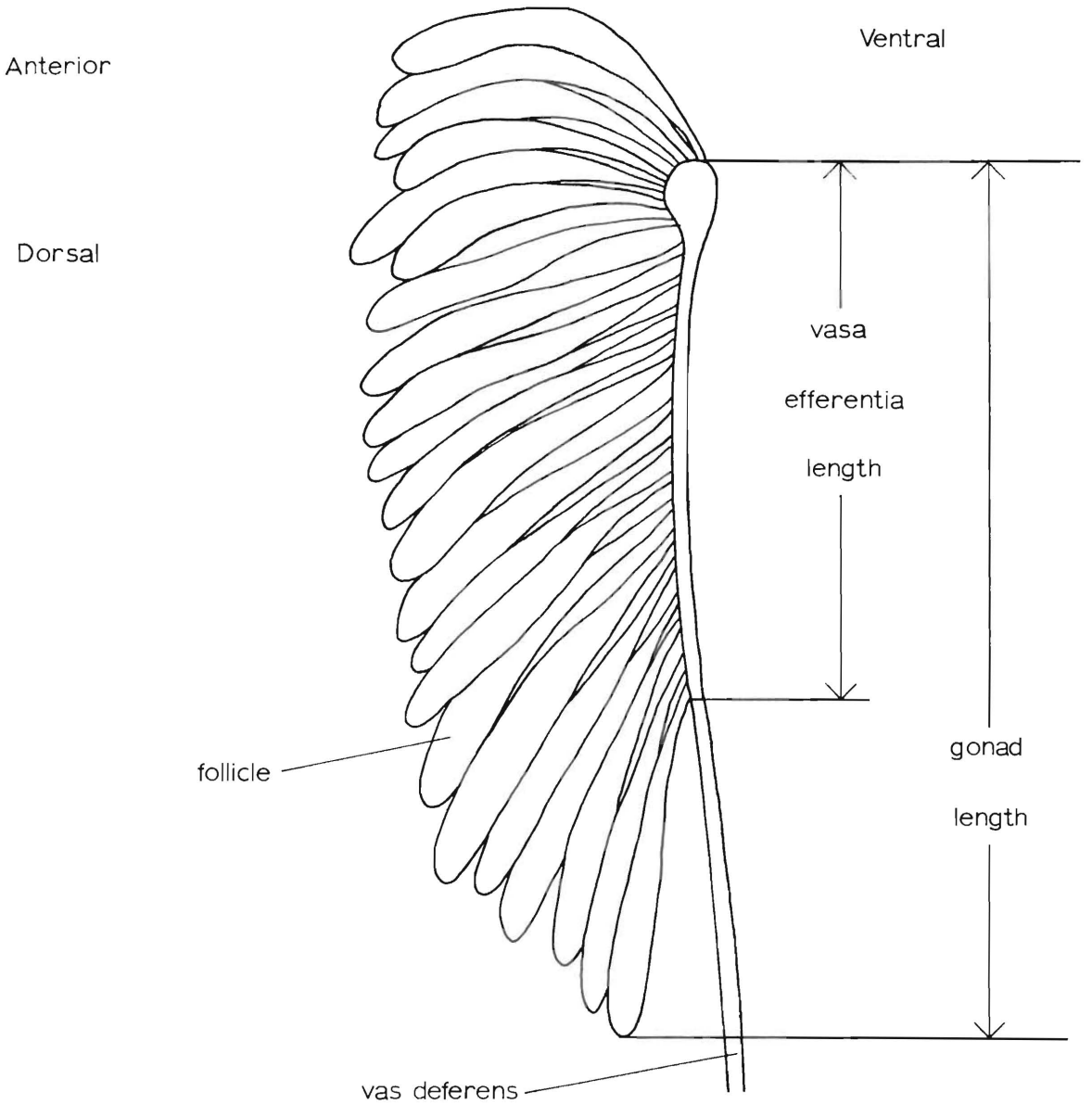

Anterior
Dorsal
Ventral
vasa
efferentia
length
gonad
length
follicle
vas deferens

Figure 3.5.1

Diagrammatic lateral view of a single testis.

they could be examined and measurements made. The results obtained are shown in Table 3.5.1.

Table 3.5.1: Gonad measurements.

Species	Mean* V.E.L. (mm)	N	Mean* G.L. (mm)	V.E.L./G.L.	Mean Follicle Number$_{a,b}$	N_f
Brachaspis collinus						
	3.8622	35	8.2525	0.468	109.83333	18
Brachaspis nivalis						
	1.7605	10	5.0240	0.35041	46.59999	5
Paprides nitidus						
	1.8836	14	4.6629	0.40395	59.50000	10
Sigaus australis						
	1.0225	4	7.1750	0.1425	25.75	4
Sigaus villosus						
	2.9925	4	8.150	0.36717	80.333	3

* = for explanation of these terms see text

N = sample size for measurements of V.E.L. and G.L.

a = folicle number is the number of testis follicles per individual

b = mean, 95% confidence limits of mean, standard deviation, coefficient of variation, Dmax by Kolmogorov-Smirnov test and sample size of this data are presented in Appendix Table XV

The testes of Sigaus australis are of the "fountain" type, those of Brachaspis collinus "intermediate" type, and those of the other species probably "fountain" type. The table also shows that there is a good correlation between the V.E.L. to G.L. ratio and follicle number. Sigaus australis has the lowest V.E.L. to G.L. ratio and the lowest number of follicles, Brachaspis collinus has the highest ratio and the largest number of follicles. The number of measurements was insufficient to make valid comparisons between populations from different areas.

3.6 Female Gonads

3.6.a General structure

The gonads of the female grasshoppers have the same general form as those of other acridids (Uvarov, 1966a) (Fig 3.6.1). The major work on the structure and development of the gonads of female Acrididae has been done by Phipps (1949, 1950, 1959 and 1962) and Singh (1958). The ovarioles are connected to two lateral oviducts which end anteriorly as blind accessory glands and unite posteriorly to form a common oviduct and vagina. A spermatheca is dorsal to the common oviduct and vagina, and opens above the vagina into the genital atrium. The terminal filaments of the ovarioles unite to form a median ligament which is

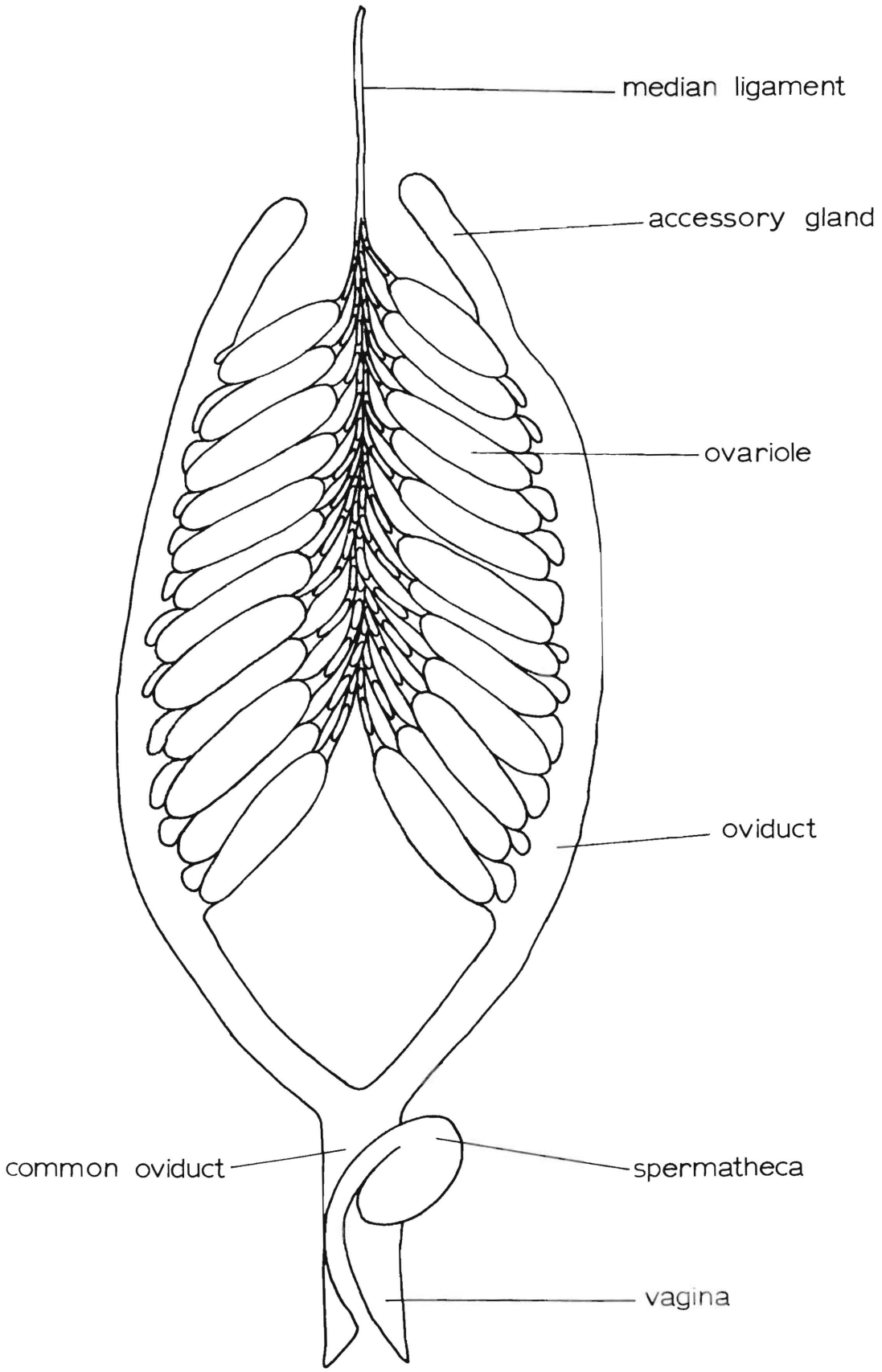

median ligament
accessory gland
ovariole
oviduct
common oviduct
spermatheca
vagina

Figure 3.6.1

Diagram of the structure of the female gonads.

attached to the aorta in the mesothorax.

Generally the terminal oocytes in each ovariole developed at the same rate, and a complete set of eggs was ovulated into the oviduct, starting with the most posterior ovarioles. No grasshopper was found with a partly filled oviduct except when eggs were being ovulated, suggesting that oviposition did not occur until all the eggs had been ovulated. The ovulated eggs caused distension of the oviducts. In Brachaspis collinus this distension caused the oviducts to reach from immediately posterior to the head capsule to the posterior end of the abdomen, causing a noticeable lengthening of the body. The eggs, plus secretions of the accessory glands (froth), were laid as an egg pod. Following oviposition the oviduct shrank to something near its original size.

The accessory gland secretions appeared in the oviducts before the eggs were ovulated, but the material did not harden while it was in the live animal (although it did harden when the animal was fixed).

On several occasions mature eggs were found free in the body cavity, having presumably been forced through the oviduct or ovariole wall.

3.6.b Ovarioles

Grasshopper ovarioles are of the panoistic type - nutritive

cells are wanting and the yolk of the egg is formed solely by the epithelium of the egg follicles (Albrecht, 1953). Ovarioles can be divided into three regions (Fig 3.6.2): (1) a slender terminal filament, (2) a germarium where division of the germ cells occurs, and (3) the vitellarium which contains the developing oocytes. Each oocyte is enclosed in a follicle. The oocyte at the base of each ovariole is the oldest and is, by convention, called egg_1. The ovarioles are attached to the lateral oviducts by a short pedicel.

The number of developing oocytes per vitellarium was found to be extremely variable. There was no correlation between the number of oocytes per ovariole and the reproductive stage (Section 3.6.d) of the animal. These observations indicate that egg rudiments may be produced throughout the life of the grasshopper. Phipps (1959) and Richards and Waloff (1954) tentatively proposed that this was the situation in the grasshoppers they studied. The latter authors suggested that physiological old age in grasshoppers is accompanied, not by a reduction in the number of egg rudiments, but by the failure to produce enough yolk for the eggs to mature.

In individual animals the number of oocytes per ovariole increased from the anterior to the posterior ovarioles. The number of oocytes per ovariole ranged from 7 to 25; but in most cases, was between 13 and 20.

Two superficially different types of ovarioles could be

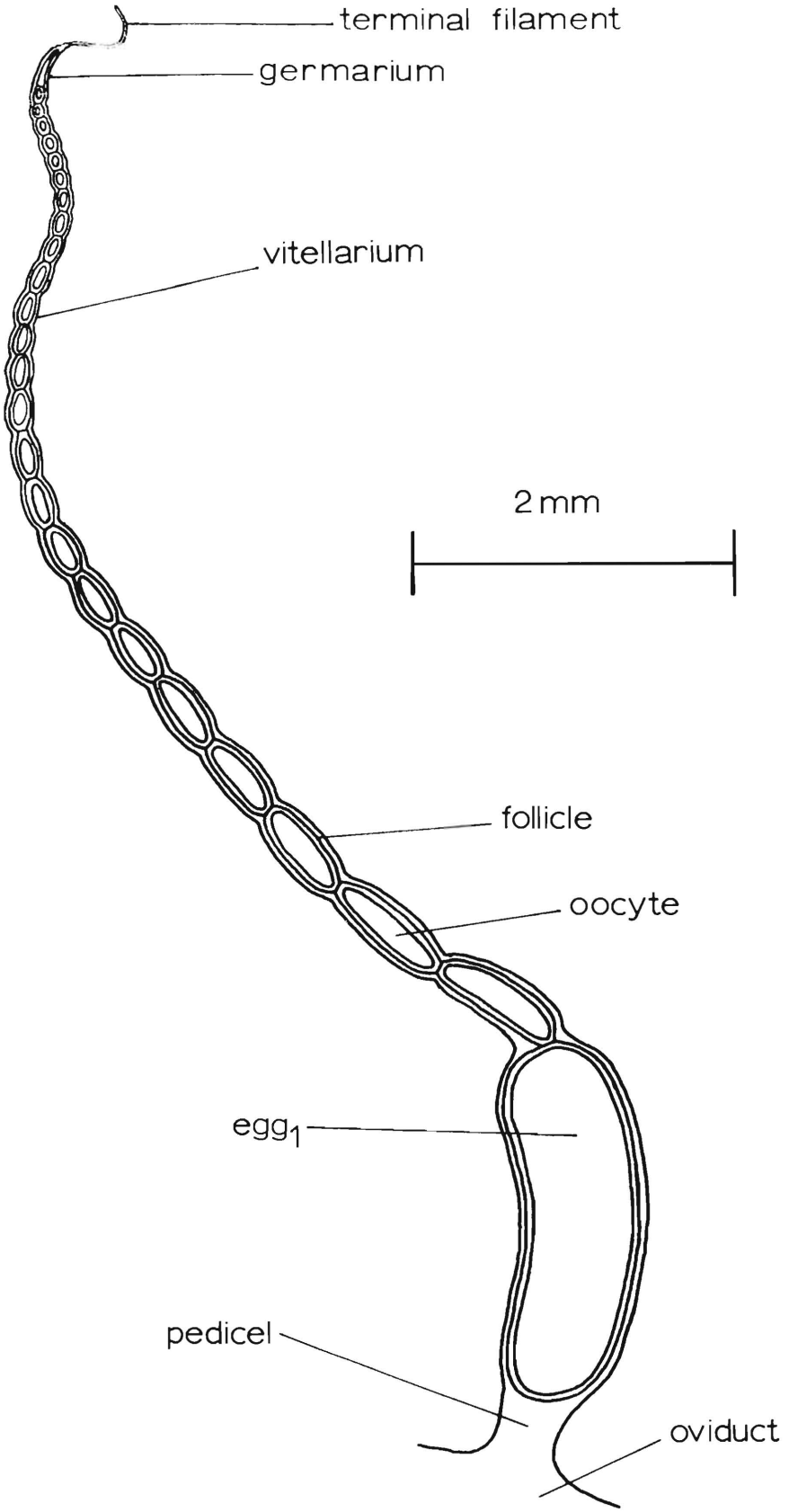

terminal filament
germarium
vitellarium
2 mm
follicle
oocyte
egg1
pedicel
oviduct

Figure 3.6.2

Ovariole from Brachaspis nivalis showing general structure of an ovariole. This ovariole is in stage III condition.

recognized in the ovaries of most grasshoppers: (1) normal ovarioles, and (2) small ovarioles (Fig 3.6.3). Normal ovarioles predominate, and are ovarioles in which oocyte development is proceeding in a "normal" manner. Small ovarioles are those which have not developed in the "normal" way. This may be brought about in two ways, egg_1 has either failed to develop, or has been resorbed before its development has been completed. Small ovarioles usually constitute 10-20% of the ovarioles in an ovary, and are responsible for the difference between the number of eggs a grasshopper lays and the number of ovarioles it contains.

The number of ovarioles per grasshopper was recorded during the examination of preserved material. An analysis of the data is presented in Table 3.6.1. The Craigieburn and Porter Heights populations of Brachaspis nivalis differ significantly in the mean number of ovarioles per animal (probability between 0.005 and 0.001 by "t" test), but the three populations of Paprides nitidus do not differ significantly (probability is greater than 0.25 by analysis of variance).

Right and left ovaries did not always contain the same number of ovarioles. The incidence and extent of this asymmetry is shown in Table 3.6.2. In most cases the two ovaries were symmetrical or differed by only one ovariole. A comparison of this table with Table 3.6.1 suggests that the percentage asymmetry is higher in the species that have larger numbers of ovarioles. Phipps (1959) observed a similar relationship in East African grasshoppers.

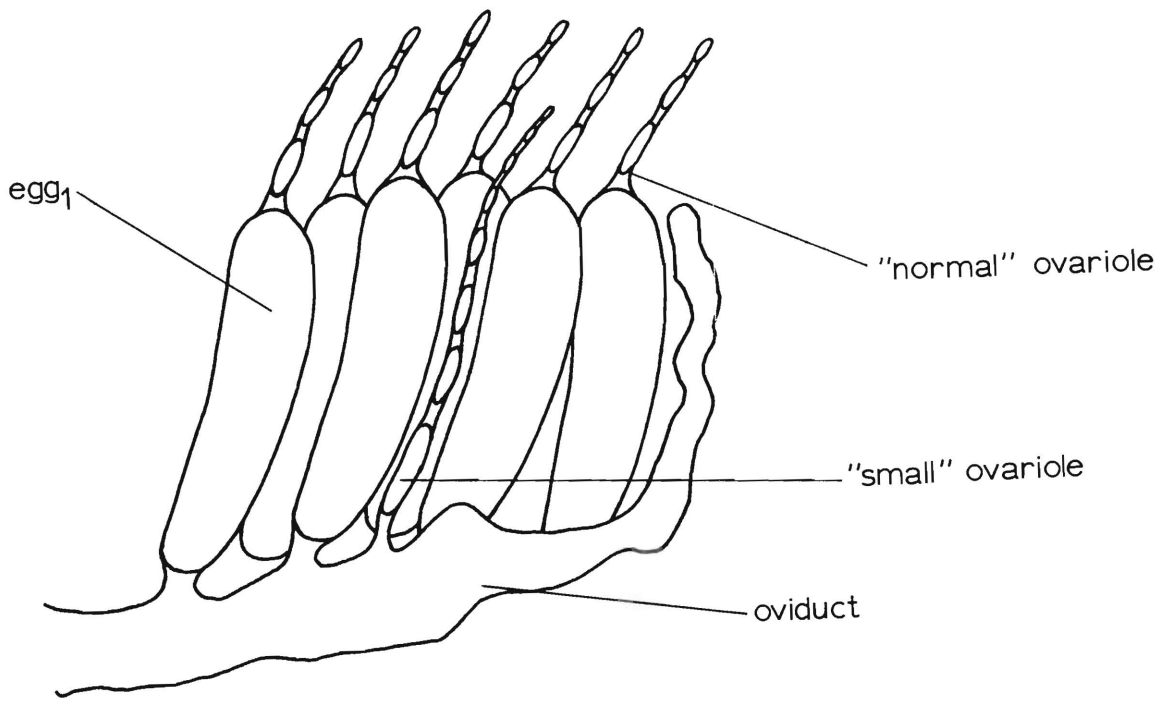

egg1
"normal" ovariole
"small" ovariole
oviduct

Figure 3.6.3

Small ovariole in an ovary otherwise at stage III.

Table 3.6.1: Mean ovariole number.

Species and area	Mean	95% confidence limits of mean		S	V	K - S D max	N
Brachaspis collinus							
Temple Basin	41.74602	40.71008	42.78194	4.11122	9.84817	0.12780	63
Brachaspis nivalis							
Craigieburn	14.00000	13.37611	14.62389	1.13389	8.09923	0.23333	15
Porter Heights	12.55556	11.87143	13.23968	1.38148	11.00295	0.26732	18
All Areas[a]	13.21212	12.52335	13.90089	1.45253	10.99391	0.16163	33
Paprides nitidus							
Craigieburn	24.50000	22.99036	26.00963	1.85164	7.55771	0.14357	8
Porter Heights	21.83333	17.81157	25.85507	6.39365	29.28387	0.25370	12
Temple Basin	23.20000	21.88730	24.51268	3.82560	16.48965	0.10958	35
All Areas[a]	23.09090	21.53712	24.64465	4.31736	18.69724	0.16433	55
Sigaus australis							
Craigieburn	38 and 24						2*
Porter Heights	38.29630	37.12268	39.46989	2.97185	7.76015	0.08714	27
Sigaus villosus							
Craigieburn	24						1*
Porter Heights	17, 22 and 23						3*

* = less than five counts in sample so actual results included in table
S = standard deviation
V = coefficient of variation
K - S D max = maximum deviation from normal by Kolmogorov-Smirnov Test
N = number in sample
a = term "All areas" includes data from all study areas

Table 3.6.2: Asymmetry in ovariole numbers between right and left ovaries.

	Difference in Ovariole Numbers						
	0	1	2	3	4	4	N
Brachaspis collinus							
frequency	15	21	13	10	3	1	63
percentage	25.81	33.33	20.63	15.87	4.76	1.59	
Brachaspis nivalis (All areas)[a]							
frequency	18	12	3				33
percentage	54.55	36.36	9.09				
Paprides nitidus (All areas)							
frequency	14	30	7	2	1	1	55
percentage	25.45	54.55	12.73	3.64	1.82	1.82	
Sigaus australis (All areas)							
frequency	11	8	5	4	1		29
percentage	37.93	27.59	17.24	13.79	3.45		
Sigaus villosus (All areas)							
frequency	1	2	1				4
percentage	25.00	50.00	25.00				

N = number in sample

a = term "All areas" includes data from all study areas, and may include data from additional areas (Section 1.7).

3.6.c Reproductive stages

Adult female grasshoppers can be placed in one of four reproductive stages. This division into reproductive stages has been used frequently in acridid studies (Phipps, 1949, 1950, 1959 and 1962; Singh, 1958 and Uvarov, 1966a). In Stage I the ovaries are immature, egg_1 is yolkless and there is no evidence that oviposition has occurred. At this stage there is a regular gradation in size between each of the developing oocytes (Fig 3.6.4(a)). Ovaries at stage I are very similar to those in sixth instar females. In Stage II egg_1 is coloured faintly yellow by the deposition of yolk and has started to increase in size. In State III egg_1 definitely contains yolk and is quite large. The oviduct contains secretions, presumably of the accessory gland, and the wall of the oviduct has thickened (Fig 3.6.2). Stage IV females have ovulated and the egg is in the oviduct, or has been laid (Fig 3.6.4(b) and (c)).

Following ovulation the follicle wall, of the now absent oocyte, shrinks and forms a ring-like structure at the base of the ovariole called a corpus luteum (Singh, 1958). This structure persists and is usually readily visible. Following oviposition the oviduct shrinks, but never completely returns to the thin-walled condition of stage I and does not completely lose the secretions of the accessory glands. These characteristics can be used to distinguish stage IV females from those at stages I,

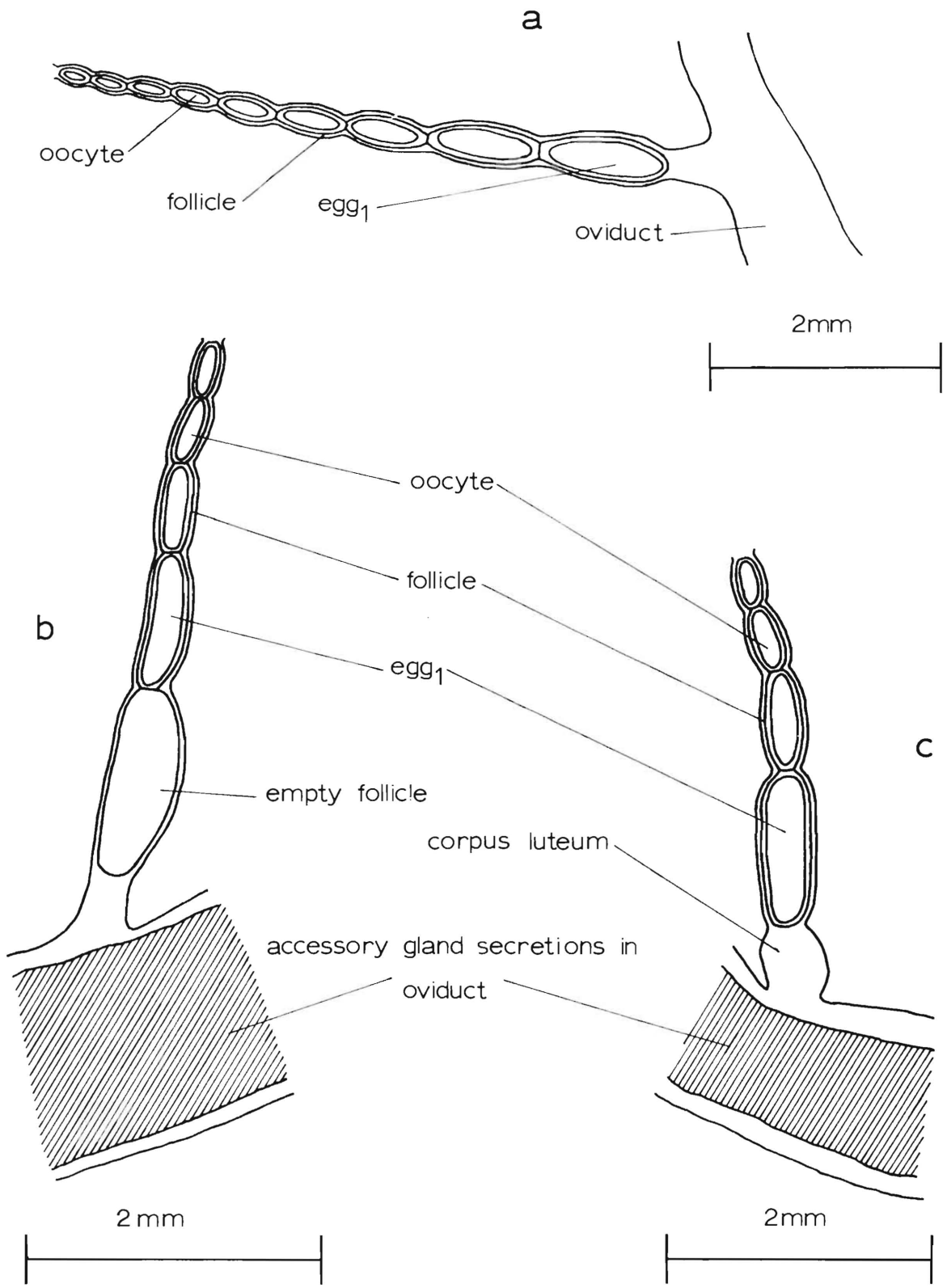

a
oocyte
follicle
egg1
oviduct
2mm
b
oocyte
follicle
egg1
empty follicle
accessory gland secretions in
oviduct
2 mm
c
corpus luteum
2mm

Figure 3.6.4

Ovarioles at different reproductive stages. (a) An ovariole at stage I. (b) Ovariole at stage IV. The oocyte has just recently ovulated and the follicle has not yet shrunken. The next oocyte now becomes egg_1. (c) Ovariole at stage IV showing appearance of corpus luteum at base of ovariole.

II and early III. However, it is difficult to distinguish individuals which are about to ovulate their first set of eggs (late stage III) from those that are about to ovulate a second or subsequent set of eggs (stage IV). In these cases the corpora lutea are very difficult to identify and none of the other characteristics of a past ovulation are visible. For these reasons the recorded incidence of females at stage III may be high at the expense of the stage IV females.

As development of egg_1 proceeds there is usually some increase in the size of egg_2; but this does not occur in all cases. There is some support for a theory that a few females go into a reproductive diapause towards the end of the snow-free season. Individuals have been examined which were obviously at stage IV (corpora lutea present, brownish secretions in oviduct, oviduct slightly thicker walled than in stage I), but these individuals had many of the characteristics of stage I females (accessory glands showing very little development, oviduct small, egg rudiments small and showing a regular gradation in size). Their ovaries appeared to have regressed further following oviposition than would normally be expected. As these individuals were only obtained from collections made late in the season it is tentatively proposed that they represent a fifth reproductive stage, of reproductive diapause.

3.6.d Accessory glands

The accessory glands, at the anterior ends of the lateral oviducts, produce secretions which are thought to form the froth of the egg pods. As the ovaries develop to maturity the accessory glands follow their developmental pattern. The extent of development is not uniform among the species studied.

In sixth instar grasshoppers and stage I adults the accessory glands are narrow blind extensions of the oviducts, containing no secretions (Fig 3.6.5(a)). As the ovaries approach maturity the accessory glands thicken, lengthen, and produce a secretion which passes into the oviduct (Fig 3.6.5(b)). In fresh specimens this secretion is colourless and fluid but in fixed specimens it is brown and rubbery.

In Brachaspis nivalis the accessory gland does not thicken, though it may lengthen slightly, as the ovary matures (Fig 3.6.5 (c)). This should result in less secretion, and the egg pods of Brachaspis nivalis are constructed with much less froth than those of the other species. Sigaus villosus exhibits accessory gland development midway between that of B. nivalis and the other three species. It is perhaps more than coincidence that lesser development of the accessory glands is exhibited by the two species restricted to screes.

Following ovulation there may be a cessation of secretion as well as shrinkage of the oviduct. If the corpora lutea are

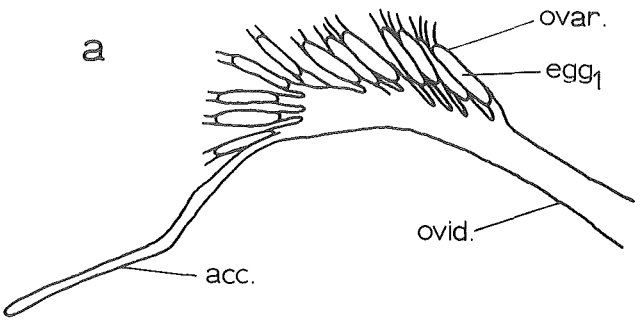
acc. = accessory gland

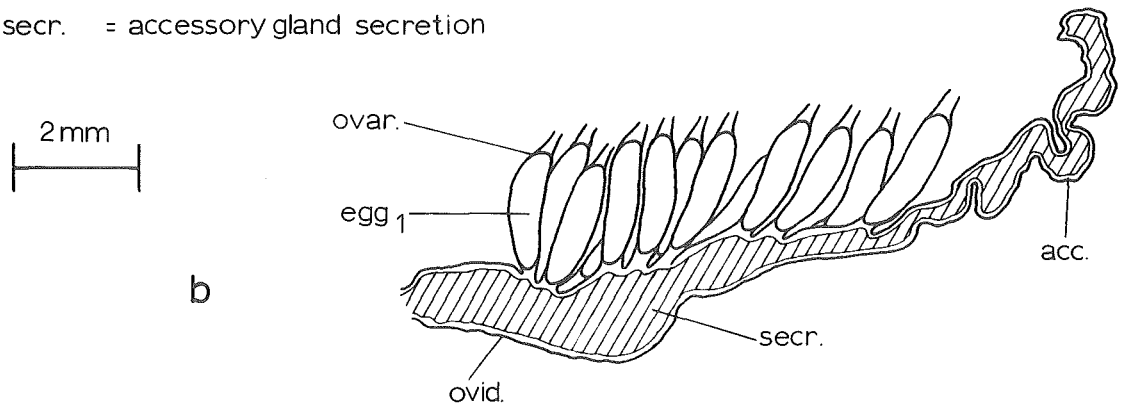
ovar. = ovariole

ovid. = oviduct

egg_1 = terminal oocyte

secr. = accessory gland secretion





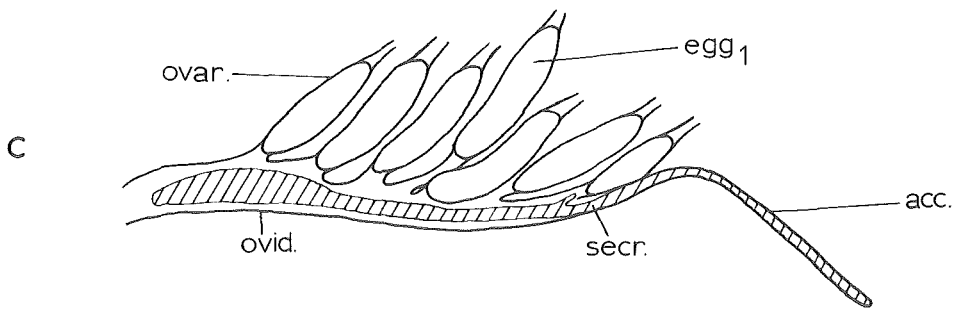


Figure 3.6.5

Development of the accessory gland. (a) Accessory gland undeveloped as it would appear in a sixth instar or stage I adult female. (b) Stage III ovary of a Paprides nitidus adult female showing well developed accessory gland. (c) Stage III ovary of a Brachaspis nivalis adult female showing poorly developed accessory gland.

not readily visible this may make it difficult to determine if a grasshopper is at stage IV or stage I, but in most cases the oviduct will still contain some secretion which can be readily identified in fixed animals.

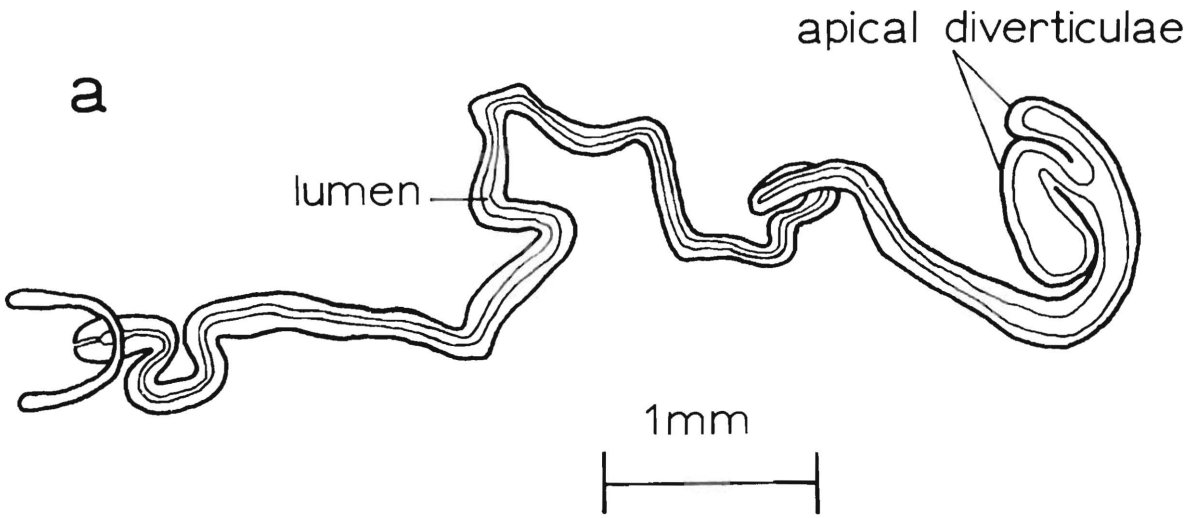
3.6.e Spermatheca

The spermatheca of all species have two apical diverticulae. This form is typical for members of the family Acrididae (Uvarov, 1966a). The shape of the spermatheca differs only in the size of the apical diverticulae in the five species studied. Fig 3.6.6 shows a spermatheca from Sigaus australis, coiled as in situ, and an uncoiled spermatheca from Paprides nitidus. The differences between species in spermatheca shape are small and of little use as a taxonomic character.

No spermatophores were observed during the examination of preserved material, or in live material following copulation.

3.7 Egg Pod Structure

Waloff (1950) defines an egg pod as "the mass of eggs, together with the secretions of the accessory glands exuded at the time of oviposition". The ability to identify an egg pod to species is ecologically useful. Descriptions of egg pods


apical diverticulae
a
lumen
1mm

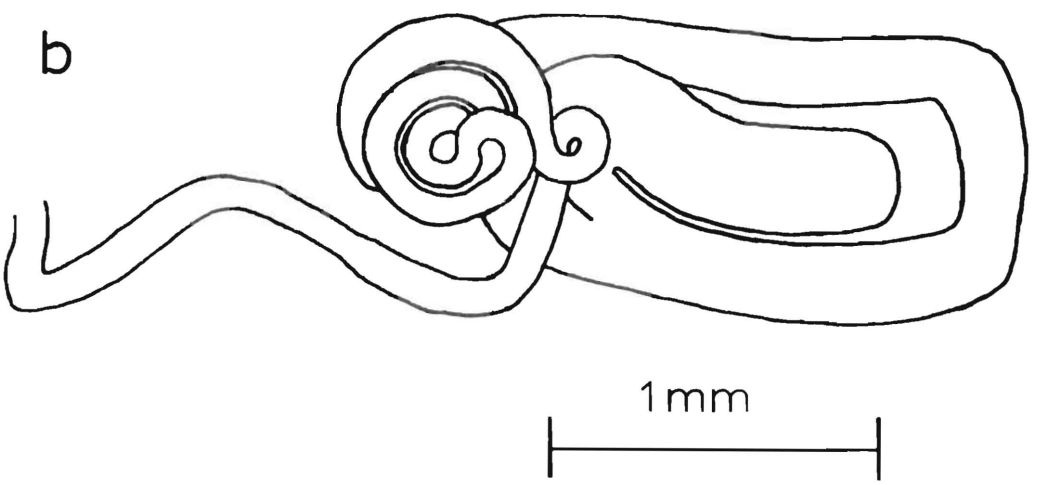

b
1mm

Figure 3.6.6

Spermatheca. (a) Uncoiled spermatheca from Paprides nitidus.
(b) Spermatheca from Sigaus australis, coiled as in situ.

(Chapman and Robertson, 1958; Onsager and Mulkern, 1963; and Waloff, 1950) use the following characters: extent and nature of the froth associated with the eggs, orientation of eggs in the pod, number of eggs in the pod, length of the pod, length and width of eggs and sculpturing of the eggs. Waloff (1950) also used the presence or absence of a lid to the pod. In the species under consideration the sculpturing of the eggs is very similar and thus of little use as a taxonomic character. The measurable characteristics of the pods are set out in Table 3.7.1. The larger sized species lay longer egg pods and have longer eggs. The egg pods of the two scree inhabiting species, Brachaspis nivalis and Sigaus villosus, contain less eggs per unit length than those of the other three species. It was stated in Section 3.6.c that small ovarioles usually constituted 10-20% of the ovarioles in a mature ovary. The small ovarioles do not produce eggs and are responsible for the difference between the number of ovarioles in an adult female and the number of eggs she lays. This difference is expressed by the ratio of egg number to ovariole number in Table 3.7.1.

All egg pods examined had the same general structure (Fig 3.7.1). They were essentially bilaterally symmetrical and none had a froth plug. Eggs were laid with their cap (posterior) end down, at an angle of about 45° to the longitudinal axis of the pod. Froth surrounded the egg mass, was present between the eggs, and formed a small pad at the anterior and of the pod.

Table 3.7.1: Egg pod data. (Mean values only.)

Species and Study areas	Pod Length[a] (mm)	Egg Length (mm)	Egg Width (mm)	No. eggs per pod[a]	Mean Ovariole No.[b]	Egg No. Ovar.No. (%)
Brachaspis collinus						
Temple Basin	22.49 (47)	6.24 (15)	1.8 (1)	34.15 (62)	41.75 (63)	82
Brachaspis nivalis						
Craigieburn	16.03 (15)	5.19 (2)	1.9 (1)	12.24 (21)	14.00 (15)	87
Porter Heights	13.38 (10)	5.27 (5)	1.4 (1)	9.83 (6)	12.56 (18)	78
All Areas[c]	15.00 (26)	5.24 (8)	1.65 (2)	11.62 (29)	13.21 (33)	88
Paprides nitidus						
Craigieburn	12.30 (2)	-	-	21.00 (2)	24.50 (8)	86
Porter Heights	12.11 (10)	5.3 (1)	0.8 (1)	16.40 (10)	21.83 (12)	75
Temple Basin	15.62 (5)	5.35 (2)	-	23.00 (7)	23.20 (35)	99
All Areas[c]	12.88 (19)	5.33 (3)	0.8 (1)	18.95 (21)	23.09 (55)	82
Sigaus australis						
Porter Heights	18.10 (3)	5.46 (3)	-	27.75 (4)	38.30 (27)	72
Sigaus villosus						
Craigieburn	29.70 (2)	7.1 (1)	-	24.00 (1)	24.00 (1)	-

Figure in brackets is the number of egg pods that made up the sample.

a = mean, 95% confidence limits of mean, standard deviation, coefficient of variation, D max by Kolmogorov-Smirnov test and sample size for this data are shown in Appendix Tables XVI and XVII

b = from Table 3.6.1 - = no data available

c = Term "All Areas" includes data from all study areas and may include data from additional areas (Section 1.7).

anterior

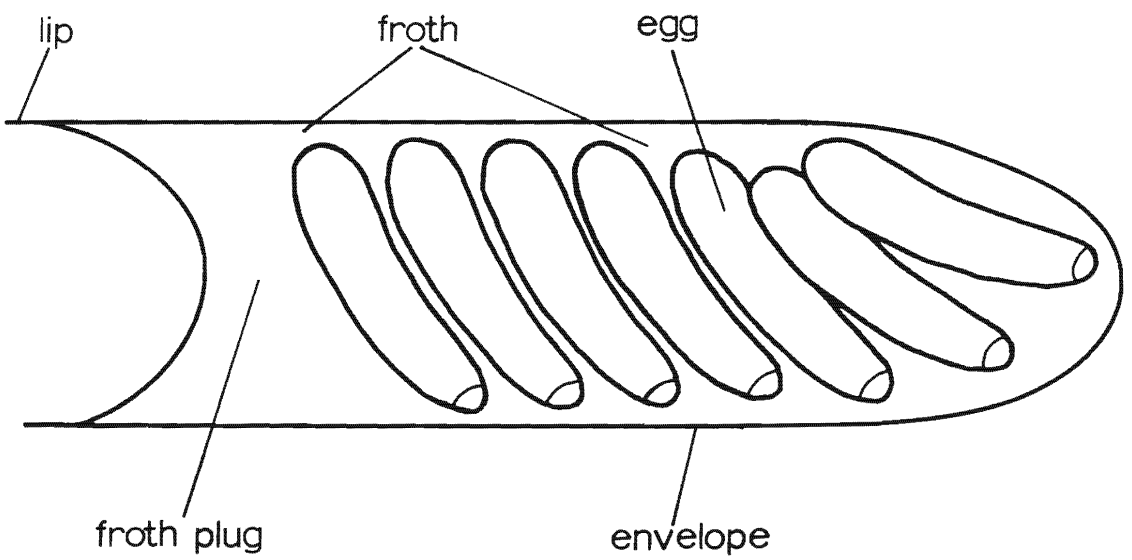


Figure 3.7.1

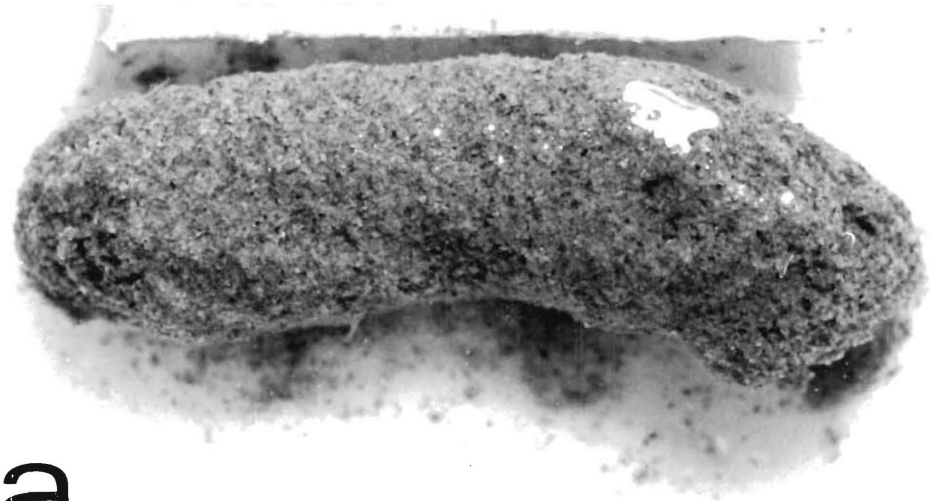
Diagrammatic sagittal section of an egg pod showing general features.

Particles of the medium in which the pod was laid adhered to the froth on the outside of the egg pod. This froth was harder than the rest and is referred to as the envelope. A lip was often present at the anterior of the egg pod, but there was no evidence of a lid in any of the species studied. Egg pods were frequently curved. All eggs were rounded anteriorly and were narrower at the micropylar (cap) end. The top of the egg pod was usually about 1 cm below the surface of the sand, but the orientation of the egg pod relative to the surface of the sand was variable.

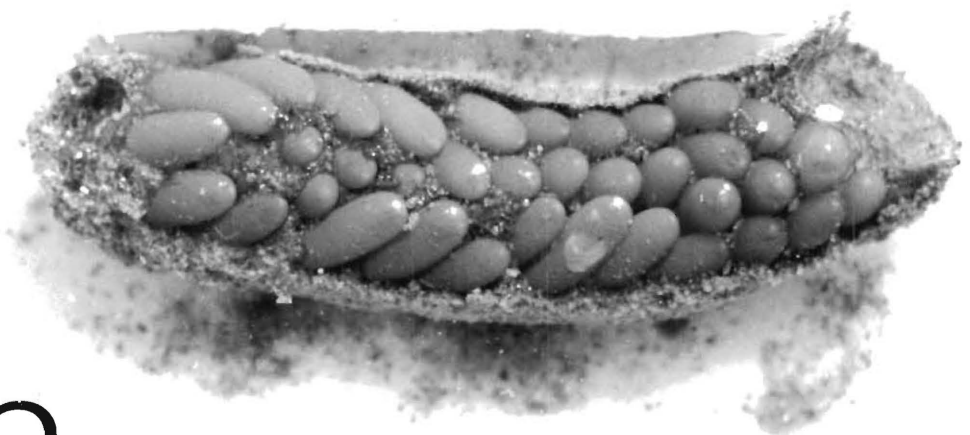
The egg pods of Brachaspis collinus were generally curved, the eggs roughly arranged into three rows, and the froth relatively thick but not hard (Fig 3.7.2). The eggs were a pale yellowish-brown colour.

The egg pods of Brachaspis nivalis were usually straight with eggs arranged in two parallel rows (Fig 3.7.3). This species has the smallest amount, and the least dense, froth associated with its eggs. The pods were very easily damaged necessitating careful handling. Compared with the other species B. nivalis had the smallest number of eggs per pod, and the broadest eggs in proportion to their length. The eggs were pale yellowish-brown. The Craigieburn and Porter Heights populations of B. nivalis differed significantly in pod length (probability by "t" test between 0.01 and 0.005), but did not differ significantly in number of eggs per pod.

Paprides nitidus had the most distinctive egg pod structure.



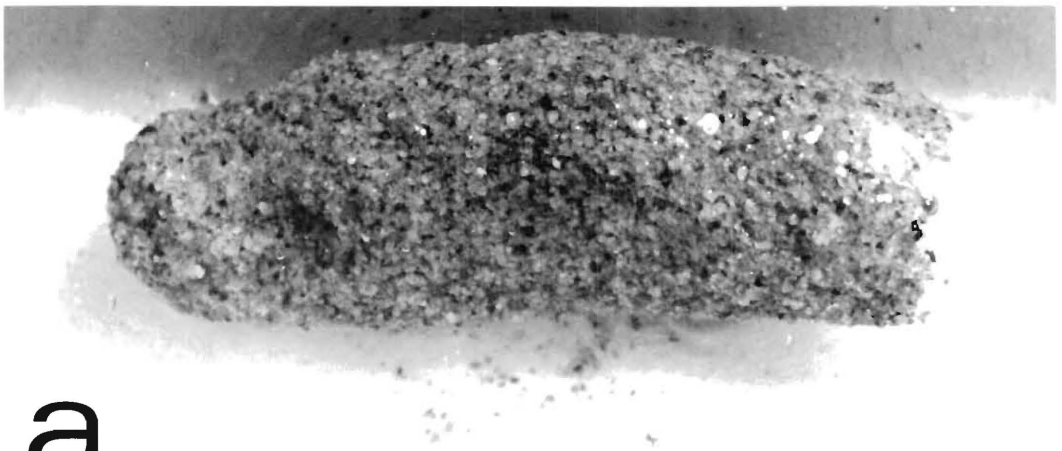
a



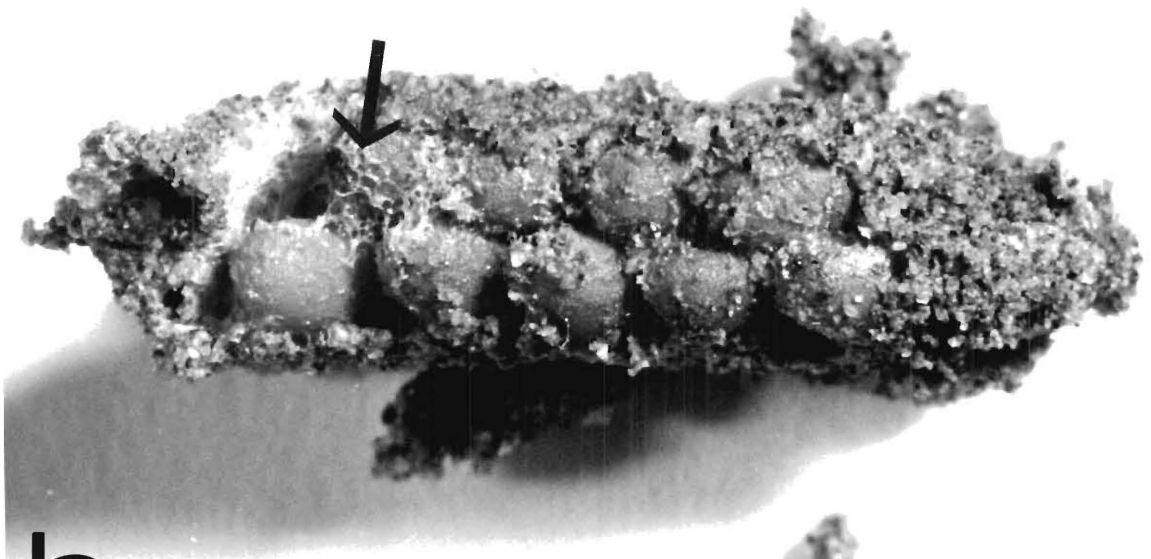
b

Figure 3.7.2

Egg pod of Brachaspis collinus. (a) Lateral view. (b) Dorsal view, with dorsal surface of envelope removed.



a



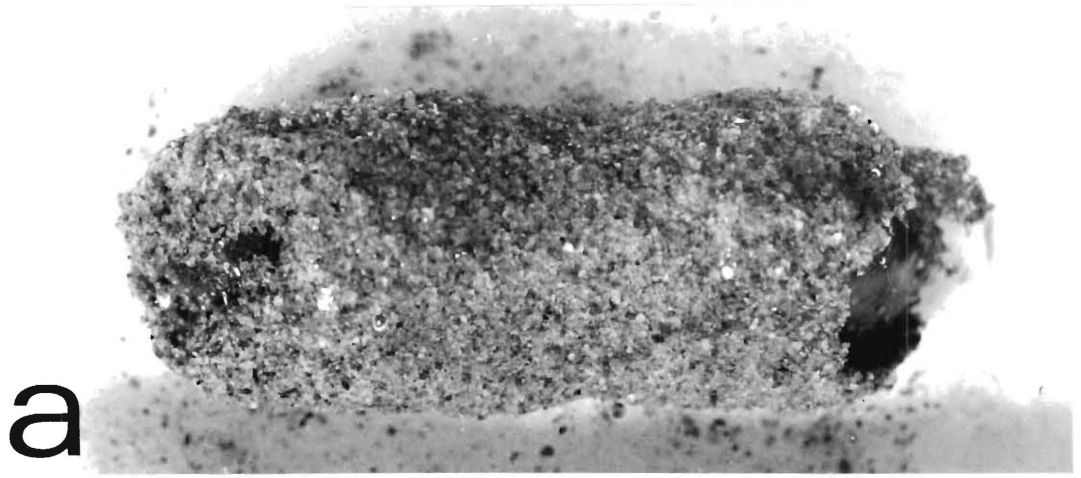
b

Figure 3.7.3

Egg pod of Brachaspis nivalis. (a) Lateral view. (b) Dorsal view, with dorsal surface of the envelope removed. Note light nature of froth (arrow).

The envelope was very hard and the individual eggs, although there was little froth between them, adhered very strongly to one another. In older egg pods the egg mass was occasionally free inside the outer envelope. This differs from the situation in other species, where the froth between the eggs was always continuous with the froth of the envelope. The arrangement of eggs usually changed from two wide at the anterior and posterior of the pod to four or five wide midway down the pod (Fig 3.7.4). The eggs of this species were thin in comparison with their length, and were a darker yellowish-brown than those of other species. The Porter Heights and Temple Basin populations of P. nitidus differed significantly in egg pod length and number of eggs per pod (probabilities by "t" tests less than 0.005 and between 0.25 and 0.01 respectively). Insufficient data were available to compare these populations with the Craigieburn population.

Information on the egg pods of Sigaus australis and S. villosus is limited because only four pods were obtained from the former and two from the latter species. The egg pods of S. australis were very similar to those of Brachaspis collinus. The froth was of the same consistency and the arrangement of eggs similar (Fig 3.7.5). Eggs of S. villosus were arranged in two rows, like those of Brachaspis nivalis, but the pods were longer and the froth was thicker. In both Sigaus species the eggs were a pale yellowish-brown, similar to those of the Brachaspis species.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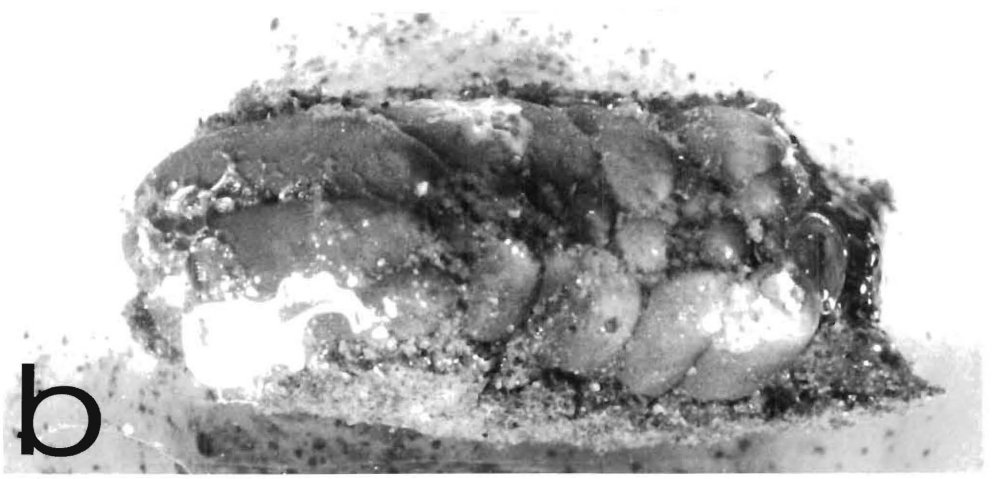

b

Figure 3.7.4

Egg pod of Paprides nitidus. (a) Dorsal view. (b) Dorsal view, with dorsal surface of envelope removed.

Figure 3.7.5

Dorsal view of egg pod of Sigaus australis with dorsal surface of envelope removed.

On the basis of these observations it is interesting to note that the two scree inhabiting species, Brachaspis nivalis and Sigaus villosus, exhibit similar egg pod structures.

It would be useful to know at what rate the gross structure of the egg pods breaks down in the field. With this information it might be possible to age egg pods found in the field. Pods kept in the laboratory showed signs of breaking down after a period of time; however, as conditions were artificial no attempt was made to apply these observations to field conditions. Investigation of egg pod breakdown in the field was not possible because of the limited availability of egg pods.

3.8 Comparison of Different Populations of the Same Species

Many comparisons were made in the preceeding subsections between species and between different populations of the same species. The latter comparisons are summarized in Table 3.8.1.

The Craigieburn and Porter Heights populations of Brachaspis nivalis were compared using seven characters. Each character is larger in the Craigieburn population, significantly larger in six out of the seven characters. This would suggest that there is a real difference between the Porter Heights and Craigieburn populations of Brachaspis nivalis.

On the basis of five characters the Porter Heights and

Table 3.8.1: Comparison of different populations of Brachaspis nivalis, Paprides nitidus, Sigaus australis and S. villosus. (In the body of the table the initials stand for the population in which the character is largest. The degree of difference found by "t" tests is shown by the asterisks following the initials - no asterisks means the populations are not significantly different, one means they are significantly different at the 5% level, two at the 1% level, and three at the 0.5% level. I.D. means insufficient data is available to give a meaningful result.)

Species	Brachaspis nivalis		Paprides nitidus		Sigaus australis	Sigaus villosus
Populations compared	CR & PH	CR & PH	CR & TB	TB & PH	PH & CR	PH & CR
Male femur length	CR***	PH	TB**	TB***	PH	CR
Male pronotum length	CR***	PH	TB*	TB*	PH	CR
Female femur length	CR***	PH	equal	PH	PH	CR*
Female pronotum length	CR***	PH	TB	PH	CR	CR
Male follicle no.	I.D.	I.D.	I.D.	I.D.	I.D.	I.D.
Ovarile no.	CR***	CR	CR	TB	I.D.	I.D.
Egg pod length	CR**	I.D.	I.D.	TB***	I.D.	I.D.
No. eggs per pod	CR	I.D.	I.D.	TB*	I.D.	I.D.

CR = Craigieburn. PH = Porter Heights. TB = Temple Basin.

Craigieburn populations of Paprides nitidus show no significant differences. However, a comparison of these two populations with the Temple Basin population shows that the latter differs significantly from the Craigieburn population in two out of four characters, and from the Porter Heights population in four out of seven characters. These results, although not definitive, do suggest that the Temple Basin population differs significantly from the other two. Peterson (1968) analysed the geographical variation in size of seven morphological characters in Paprides nitidus. Using notch width of the female subgenital plate Peterson placed the various geographical samples he examined into five population groups. Specimens from the Temple Basin study area are in a different group from those in the Craigieburn and Porter Heights study areas. The results obtained during this study support Peterson's hypothesis that only restricted exchange of genetic material occurs between populations of Paprides nitidus at Arthurs Pass (Temple Basin study area) and on the Craigieburn Range (Craigieburn and Porter Heights study areas).

No significant differences were found between the Porter Heights and Craigieburn populations of Sigaus australis. The Porter Heights and Craigieburn populations of Sigaus villosus differed significantly in only one character out of four (female femur length). The Porter Heights and Craigieburn populations of both Sigaus species are not here considered to be significantly different.

Section 4

LIFE HISTORY INFORMATION

4.1 Introduction

The only published account of the life history of a New Zealand alpine grasshopper species is that of Batcheler (1967). Batcheler found that Brachaspis collinus at Cupola Basin had a very flexible life cycle, with development from hatching to maturity probably taking about three years. The species was able to overwinter in most stages of its life history.

Information recorded during this study is used in this section to build a picture of the life cycles of the New Zealand alpine grasshoppers. More data were obtained for Brachaspis collinus than for any of the other species obtained. However, despite a lack of data it has been possible to construct a proposed life cycle for four of the five species studied.

4.2 Seasonal Incidence of Instars

Experiments in the laboratory showed that at the temperature under the snow (approximately $0^{\circ}C$) grasshoppers were unable to move. Moulting and hatching would not, therefore, be expected to occur under the snow. During the thaw the ground would be sodden with snow meltwater at a temperature just slightly above $0^{\circ}C$ and the utilization of radiant energy to convert the snow to water would keep the air temperature low. Under these conditions

neither hatching nor moulting would be expected to occur. Thus, the instars collected while the thaw was occurring would be expected to be representative of those that had overwintered.

It is clear from Table 4.2.1 that representatives of nearly every instar of Brachaspis collinus were collected during the thaw of 1967 at Temple Basin. The male instars that are missing are represented by their female equivalents, and the converse. These results suggest that all instars are capable of overwintering.

The collections made during the 1968-69 season suggest that all instars of both sexes of Brachaspis collinus were present at Temple Basin throughout the snow-free period. The incidence of first instar individuals in the 1968-1969 collection is markedly different from that in the 1967-1968 collections. This is probably a result of their distribution in the field. First instar grasshoppers occur in clusters in the field; consequently their presence in a collection depends to a considerable extent on collecting experience and chance. The monthly collections do not accurately represent the frequency of each instar.

Similar evidence collected for Brachaspis nivalis, Paprides nitidus and Sigaus australis, although less extensive than that for Brachaspis collinus, suggests that all instars of these four species are present throughout the snow-free season and can overwinter. Insufficient evidence is available to determine if Sigaus villosus also falls into this category.

Table 4.2.1: Breakdown of specimens of *Brachaspis collinus* collected at Temple Basin during 1967-1968 and 1968-1969 snow-free seasons.

Sex and Instar		1967		1968			1968		1969				
		Nov	Dec	Jan	Feb	Mar	Nov	Dec	Jan	Feb	Mar	Apr	May
Male	I								1	6	1		3
	II	8	3	3	2	2		7	11		1		5
	IIIA	2	5	1	6	3	1	2	6	2	2		
	IV	1	3	2	5	3	1	4	4	1	1		2
	V	3	2	1	4	9		1	11	1	2		4
	VI	4	6	3	3	7	1	1	11	4			5
	adult	10	26	9	11	25	18	7	42	27	10		15
Female	I	3				2		2	1	5	2		2
	II	5	4			1		3	10	1	6		
	IIIA		3		3		2	1	5	2			
	IIIB	1	2	1	6	3		3	5	1			1
	IV	1	1		2	10		3	6	2			
	V	1	2		3	4		2	7	2			4
	VI		1		4	7		1	18	1	2		1
	adult	9	20	7	1	27	9	6	13	27	10		6

4.3 Nature of Overwintering in Juvenile and Adult Grasshoppers

Overwintering in grasshoppers can be of two types, diapause or quiescence. Quiescence was the term suggested by Shelford (cited in Andrewartha, 1952), to cover the situation in which development is temporarily inhibited by an unfavourable environment and may be resumed as soon as the hindrance is removed. Diapause, too, is a suspension of growth or development, but its initiation and termination are more complex than those associated with quiescence, and development is not necessarily resumed when conditions become favourable.

Evidence gathered during this study suggests that the New Zealand alpine grasshoppers overwinter in a state of cold induced quiescence. In June, 1967, there was a fall of snow at Temple Basin which completely covered the area with snow. Seven days later the snow had melted somewhat and small patches of scree were exposed. On one of these a Brachaspis collinus fifth instar male was captured and some first or second instar individuals observed. Mr. D. W. Tattle collected three grasshoppers (Brachaspis collinus female adult and male adult, and Paprides nitidus female adult) in July, 1968 at 4900 ft on Amuri Ski Field. The grasshoppers were found on snow near a large rock around which the snow had melted (presumably allowing the grasshoppers to emerge from under the snow). Grasshoppers, belonging to a variety of species and instars, kept in an outdoor cage in

Christchurch (altitude 50 ft) during late autumn and winter 1968 did not go into diapause.

In the first two examples given above, the active grasshoppers were found early in the winter. If the grasshoppers overwintered in a state of diapause a minor thaw of snow early in the winter or the melting of snow from around a rock should not have been sufficient to break diapause. Furthermore, specimens caged outside at Christchurch would probably have entered diapause if this was the mode of overwintering in the field.

4.4 Seasonal Incidence of Reproductive Stages and Oviposition

Ovarian development of adult female grasshoppers can be divided into four stages. These reproductive stages were described in Section 3.6.c. The ovaries of recently moulted adult females develop from the immature stage I condition through stage II to stage III before ovulating and becoming stage IV. It was found convenient to recognise an additional reproductive stage "IV+" for stage IV females which had ovulated but still retained the eggs in their oviducts. Stage IV+ females have just left stage III and are about to oviposit.

Information presented earlier in this section suggests that adult females were present throughout the snow-free season and were able to overwinter. To relate the reproductive state of the

adult females to their physical presence the seasonal incidence of reproductive stages III, IV+ and IV in the field, and the seasonal incidence of oviposition were examined. The incidence of stage I and II females was never high in any of the collections and will not be considered in the ensuing discussions.

Adult females at reproductive stages III, IV+ and IV were present in collections made during spring thaws (see Table 4.4.1). These grasshoppers had only recently lost their winter covering of snow, and as the thaw was still continuing low temperatures would have prevented any rapid development of ovaries. This suggests that stage IV females overwinter and that either stage III females overwinter or ovaries can develop slowly under the snow. The stage IV+ females may have emerged from the snow either at stage IV+ or at stage III and since ovulated.

Data on the incidence of reproductive stages during the snow-free season are recorded in Table 4.4.2. The 1966-1967 collections of Brachaspis collinus all contained females at stage IV and all except those for May contained specimens at stage IV+. Females at stage III were, however, poorly represented. The 1968-1969 collections of Brachaspis collinus and Paprides nitidus showed a higher incidence of stage III females. These data suggest that stage III, IV+ and IV females may be present throughout the snow-free season.

This incidence of stage III and IV+ females suggests that for most of the snow-free seasons there were grasshoppers present

Table 4.4.1: Adult female grasshoppers of stages III, IV+ and IV collected during spring thaws.

Species and Study Area	Reproductive stage III	IV+	IV	N*
Collected October 1969				
Brachaspis collinus				
Temple Basin	3	1	3	7
Brachaspis nivalis				
Craigieburn	7	-	3	10
Porter Heights	2	3	3	8
Paprides nitidus				
Craigieburn	3	-	2	5
Porter Heights	8	-	-	8
Temple Basin	2	-	-	3
Sigaus australis				
Craigieburn	2	-	-	2
Porter Heights	19	1	3	24
Collected November 1968				
Brachaspis collinus				
Temple Basin	3	-	1	4
Paprides nitidus				
Temple Basin	3	-	1	4

N* = the total number of adult females collected

Table 4.4.2: Incidence of stages III, IV+ and IV among adult female field grasshoppers during the snow-free season.

Species and Stage	Nov	Dec	Jan	Feb	Mar	Apr	May
Collected 1966-1967 Season							
Brachaspis collinus							
Stage III		-	2		4	-	-
Stage IV+		2	2		1	1	-
Stage IV		7	2		3	1	1
Total number adult females collected		9	7		8	2	1
Collected 1968-1969 Season							
Brachaspis collinus							
Stage III	3	2	2	2	-		
Stage IV+	-	-	3	-	1		
Stage IV	1	-	-	10	3		
Total number adult females collected	4	2	6	12	6		
Collected 1968-1969 Season							
Paprides nitidus							
Stage III	3	2	2	-	1		
Stage IV+	-	-	-	1	-		
Stage IV	1	2	-	2	3		
Total number adult females collected	4	4	2	3	4		

in the field capable of laying egg pods. This was supported by records of the incidence of oviposition in laboratory grasshoppers (Table 4.4.3). Although obtained under laboratory conditions, these records do suggest there is a potential for oviposition present in the Brachaspis collinus and Brachaspis nivalis populations for the majority of the snow-free season.

Table 4.4.3: Relationship between the presence of adult females in the laboratory and the occurrence of oviposition in the laboratory. (A positive result is indicated by an "X".)

Species	Months							
	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Brachaspis collinus				1966-1967 Season				
Adult females caged*	X	X	X	X	X	X	X	
Eggs laid		X	X	X	X	X		
Brachaspis collinus				1967-1968 Season				
Adult females caged*	X	X	X	X	X	X	X	
Eggs laid	X	X	X	X	X	X	X	
Brachaspis nivalis				1966-1967 Season				
Adult females caged*		X	X	X	X	X	X	X
Eggs laid		X	X	X		X	X	X

* = "Adult females caged" means that adult females were in cages in the laboratory during the indicated months.

Batcheler (1967) suggested that peaks of oviposition activity by Brachaspis collinus occurred at Cupola Basin. Records made during the present study suggest that oviposition by Brachaspis collinus occurs throughout the snow-free season at Temple Basin, but data are insufficient to show if oviposition peaks do, or do not occur.

In the field, oviposition would not be expected to occur much later than April. Low air temperatures would slow down the metabolic, and hence developmental, rate of the grasshoppers, soil temperatures would be low and the ground possibly frozen. Consequently, the May and June ovipositions in the laboratory (Table 4.4.3) were probably a product of the higher temperatures in this environment. This suggests that in some females maturation of eggs and oviposition may continue as long as conditions are favourable.

Of the few dead adult female grasshoppers collected in the field, the majority were at late stage III or stage IV+. This suggests that some females continue developing eggs until they die. Females at stages III and IV+ contain very little fat body and thus have very little reserve food and would be susceptible to starvation during the winter or other periods of prolonged cold. Dissections suggested there was a reproductive diapause towards the end of summer in some stage IV adults (Section 3.6.c), and showed that stage IV females were present at the thaw (Table 4.4.1). Grasshoppers in reproductive diapause would be able to

build up fat reserves in order to survive over a long winter or cold period. These observations suggest that some adult females (probably the younger ones) prepare for winter by going into reproductive diapause, while others keep producing eggs, at a rate determined only by the effect of the climate on their metabolism, until their food resources are exhausted and they die.

4.5 Multiple Oviposition

Batcheler (1967) suggested that the specimens of Brachaspis collinus at Cupola Basin laid only one pod of eggs before dying. Evidence gathered for the present study suggests that this is not the case in the Canterbury alpine grasshoppers. Most adult females kept in the laboratory laid only one pod of eggs before dying, but definite instances of multiple oviposition were recorded. A Brachaspis collinus adult female kept at 38°C laid two pods of eggs in nine days. Two Brachaspis nivalis adult females kept at 30°C laid eight pods of eggs, of which six were laid in ten days. Six B. nivalis adult females kept at room temperature laid ten pods of eggs over a period of 66 days. Since multiple oviposition can occur in the laboratory it would be expected to occur also in the field.

The ovarioles of all the female ovaries examined contained at least nine, and up to 26, developing oocytes in their

vitellaria. This suggests that the females of all species possess a potential for multiple oviposition. It is suggested that multiple oviposition, far from being an occasional occurrence, is the norm. If it was not the norm there would be little advantage in stage IV females overwintering, or in the development of a second set of eggs by stage IV females, and the high proportion of stage IV females in the population throughout the year would be difficult to understand.

4.6 Egg Development and Hatching

Grasshoppers caged in the laboratory were the principle source of eggs in this study. However, a few of the eggs used in experiments were collected in the field. When egg pods were obtained they were placed on damp sterile sand (or damp vermiculite) in a plastic petri dish. Eggs handled in this way and given a regular dousing with distilled water generally remained in good condition. The chief hazard was infection by fungus.

Eggs for embryological examination were fixed whole in Carnoys fixative (glacial acetic acid - 25cc, chloroform - 75cc, absolute alcohol - 150cc) for four to six hours, bathed in absolute alcohol for two 15 minute periods, and finally stored in 70% alcohol. Before fixation eggs were usually soaked for about five minutes in 10% sodium hypochlorite (Slifer, 1945).

This removed the chorion and often made it possible to observe the embryo without having to dissect it out. Embryos to be mounted were dissected out, stained for five to seven minutes in 1% Chlorazol Black E, dehydrated and mounted in Canada Balsam (Craig, 1967). Handling of eggs and embryos during fixing and staining was minimized by placing them in short lengths of one centimeter diameter plastic tubing with copper gauze heat-sealed to the base. The tubes did not affect the staining process.

Early in the study it became obvious that the eggs of the New Zealand alpine grasshoppers went into an obligatory diapause. Embryological development, where there is an obligatory diapause, can be conveniently broken up into three stages: pre-diapause development, diapause and post-diapause development. Embryological investigations made in early 1970 as part of this study established that diapause occurred at the end of anatrepsis (Fig 4.6.1(d)). Several pods of eggs which had been laid up to 24 months previously, were still apparently healthy and contained embryos, all at this diapause stage.

Two experiments were designed and implemented to gain some information on the time required for embryos to reach the diapause stage. In each experiment, design of the sampling program was based on the assumption that developmental rate would be similar to that found by Van Horn (1966) for Aulocara elliotti and the sampling period modified to allow for temperature differentials. Diapause was considered to be reached when embryos had reached

the end of anatrepsis (Fig. 4.6.1), and their eyes had darkened. This was noted to be the condition of diapause embryos in other eggs examined and is consistent with the criteria used by Van Horn to indicate diapause.

Six Brachaspis collinus egg pods laid in the laboratory during the period February 17-24, 1970, were kept at 26-28°C and samples taken according to a predetermined schedule. The results of this experiment (Table 4.6.1) show that at the experimental temperature, Brachaspis collinus eggs reach diapause stage in approximately 30 days.

Table 4.6.1: Pre-diapause development of Brachaspis collinus embryos at 26-28°C.

Pod No.	Observations
1	All embryos older than 30 days were in diapause. Eyes were starting to darken at 25 days.
2	3 out of 4 embryos in diapause at 29 days, 1 out of 5 in diapause at 25 days. All embryos older than 40 days in diapause.
3	Eyes starting to darken at 25 days, and still darkening at 28 days. All in diapause after 40 days.
4	Eggs did not develop.
5	All in diapause at 38 days. Eyes still light at 27 days.
6	Eggs did not develop.

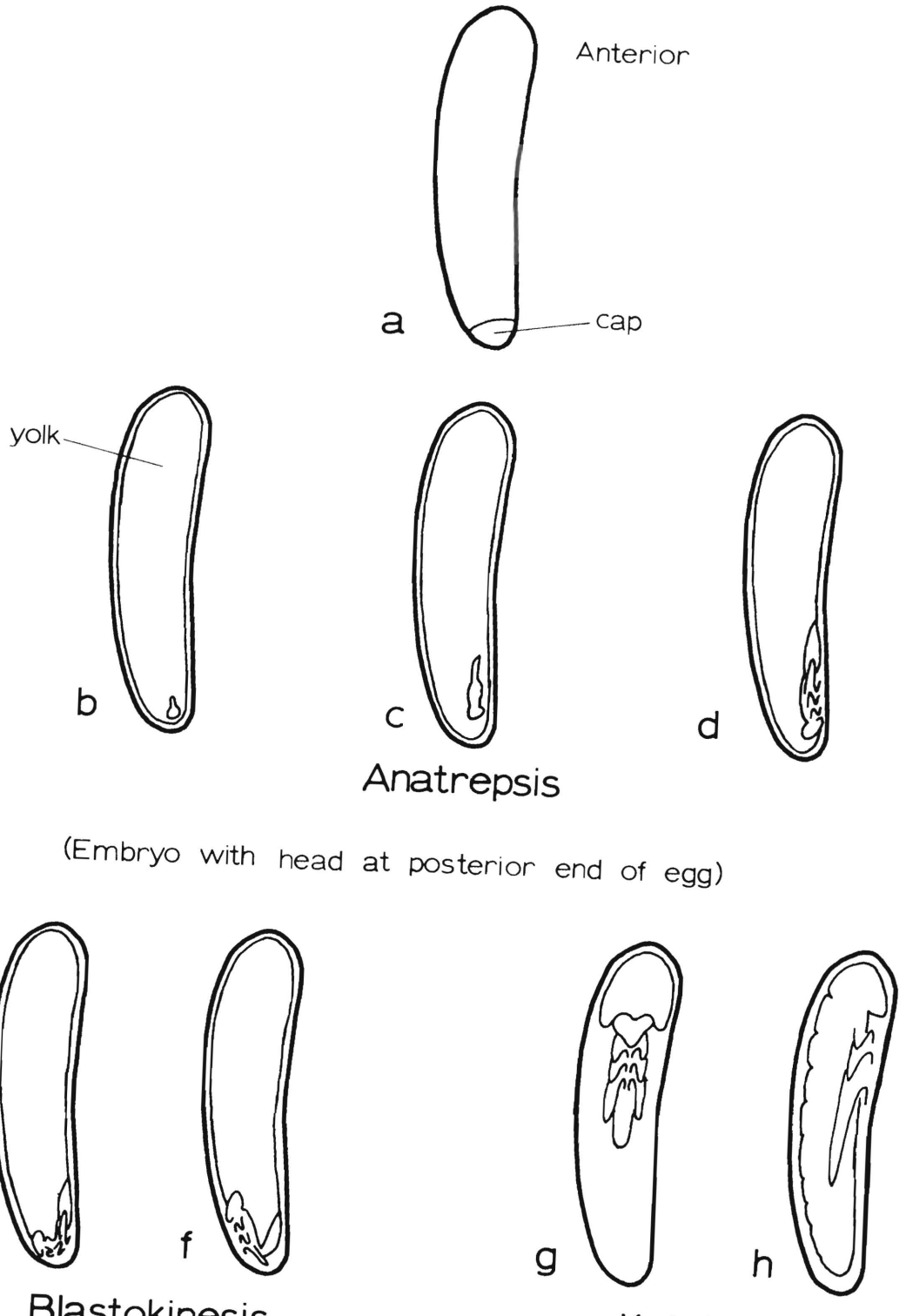

Anterior
a
cap
yolk
b
c
d
Anatrepsis
(Embryo with head at posterior end of egg)
e
f
Blastokinesis
(Embryo turning)
g
h
Katatrepsis
(Embryo with head at anterior end of egg)

Figure 4.6.1

Diagram of development in the grasshopper egg. (a) The orientation of the egg in this diagram is maintained in the following diagrams. (b) - (h) Stages in embryonic development of a grasshopper. (d) The stage at which diapause occurs in Brachaspis collinus, B. nivalis, Paprides nitidus and Sigaus australis.

(After Uvarov 1966a)

In the second experiment seven egg pods of Paprides nitidus and one egg pod of Brachaspis nivalis, laid in the laboratory between December 26, 1969 and January 1, 1970 were kept at room temperature (20 ± 5°C). The B. nivalis eggs reached diapause stage sometime between 33 and 49 days from laying. 33 day old embryos still had pale eyes but apart from this were very similar to diapause embryos. Diapause was probably reached in about 40 days. One embryo of Paprides nitidus, from a sample of four, had reached diapause stage in 54 days, while four embryos from another pod had not reached this stage after 56 days. The Paprides nitidus eggs had developed at a slower rate than anticipated. When the experiment was terminated after 56 days only the one embryo of this species had reached diapause.

The results of the previous two experiments show that the rate of pre-diapause development is a function of temperature and species.

Very few eggs hatched in the laboratory. The hatches that did occur are shown in Table 4.6.2. Group A hatches resulted from an experiment in which ten egg pods, which had been kept at room temperature for at least 60 days and could be assumed to be in diapause, were split in two. One set of half pods was put in the refrigerator at 2-5°C, and the other set was kept at room temperature (20 ± 5°C). When the selected period of cold treatment for each half pod was completed it was removed from the refrigerator. The two halves of each pod were then put at the

Table 4.6.2: Laboratory hatches

Group	Species	Pre-cold treatment Days	Temp °C	Cold treatment Days	Temp °C	Days to hatch Days	Temp °C	%Hatch / Number Hatched
A	Brachaspis nivalis	84	R*	35	5	15	28	100
	" collinus	81	R	35	5	54	R	94
	" "	83	R	35	5	54	R	53
								Number Hatched
B	Sigaus australis	? field		54	fridge*	24	R	34
	Brachaspis collinus	unknown time in field				30-34	R	31
						111	R	2
						148	R	1
								% Hatch
C	Brachaspis collinus	-		-		216	various	17
	" "	-		-		223-239	R	20
	" "	-		-		246	R	9
	" "	-		-		212-7	R	50
	" "	-		-		222-8	R	29
	" "	-		-		220-6	R	21
	" "	-		-		300	R	11
	" nivalis	-		-		270-4	R	87
	" "	-		-		315-9	R	?

Table is explained in text. Group B eggs were collected in the field, the rest were laid in the laboratory. Group C eggs were not given any cold treatment. % hatch is the percentage hatch per pod.

* R = room temperature = 20 ± 5°C
fridge is the refrigerator at the Forest Service Cave Stream field station

same temperature (room temperature or 28°C). The three half pods that hatched make up group A. All three had had cold treatment. The percentage of eggs in each half pod that hatched was high. Other eggs which received almost identical treatment to the group A eggs did not hatch. This suggests that all the eggs in a pod possess similar requirements for diapause termination and that these requirements vary from pod to pod. A maternal effect could also be having an influence.

The group C hatches were from eggs that had been kept in the laboratory at room temperature from the time they were laid. The time taken to hatch was very long (over 200 days) and the percentage hatch was, in most cases, quite low. These results suggest that the eggs that hatched were those which had somehow managed to terminate their diapause. These hatches show that there must be small differences in diapause termination requirements between the eggs in one pod.

The group B hatches were from eggs collected in the field in November, 1966. Their appearance, when collected, would suggest they had been laid the previous winter as the gross pod structure had broken down. Sixty-five eggs hatched within 34 days at room temperature. A comparison of this time with that for group A hatches at room temperature would suggest that the group B eggs had terminated diapause and had partially completed post-diapause development when collected. This development was completed in the laboratory. The history of the Sigaus australis eggs shows

that they are able to withstand a period of freezing during development.

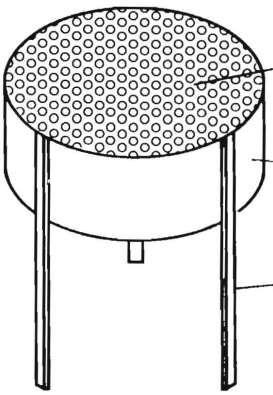
In an attempt to obtain a larger hatch and some information on post-diapause embryonic development, several egg pods from assorted species and with assorted past histories (but all having spent at least 80 days at room temperature), were refrigerated (at 2-5°C) for 16 months. At the end of this period dead eggs were discarded, a sample from each pod fixed and the remaining eggs put at 27-30°C. Samples were taken and fixed at intervals over the next 20 days, and on the 21st day all remaining eggs were fixed (the 20 day period was chosen because Brachaspis nivalis eggs hatched after 15 days at 28°C - Table 4.6.2). Examination revealed that in all cases embryos were at the diapause stage when removed from the refrigerator and in the majority of cases no development occurred during the following 20 days. The exception was one pod of Brachaspis collinus eggs which were ready to hatch after 21 days. The embryos were turning at four days and had completed turning at twelve days.

This experiment suggests that the cold treatment provided was not of the required type for termination of diapause. A period of below freezing temperatures may be necessary to terminate diapause in the New Zealand alpine grasshoppers. This could not be tested because of lack of eggs. Temperatures just above freezing point were chosen for experiments because they had been most effective in published studies (Riegert, 1967; Uvarov, 1966a).

An experiment was designed to compare the development of eggs at Temple Basin (45-4600 ft), Christchurch (50 ft), and in the laboratory. Five stations were set up: Station A was at Temple Basin (4600 ft) on a site covered with snow throughout the winter. Station B was also at Temple Basin (4500 ft) on a site that was only marginally covered with snow throughout the winter. Stations C and D were located next to one another in a garden in Christchurch with no recent history of insecticide spraying. Station E was at room temperature in the laboratory.

At stations A-D the eggs were placed approximately 1 cm below the soil surface and the site was covered by an emergence cage (Fig. 4.6.2) to trap hatched grasshoppers and to protect eggs and hoppers from predation by birds. All the eggs used in the experiment were laid in the laboratory and prior to being placed at the various stations had been kept at room temperature for at least 80 days and were assumed to be at diapause stage. Eggs were placed at stations A and B on May 25, 1969, and at stations C and D on June 14, 1969. Each station was supplied with a complete egg pod, so that rate of pod breakdown could be studied, and with part of an egg pod so that results could be compared between areas. The eggs were removed from stations A and B, and C and D on February 12, 1970, and February 13, 1970 respectively and along with the eggs from station E fixed in Carnoys. Station B was disturbed in the field and the emergence cage removed; only a few eggs were recovered.

Bird Protector

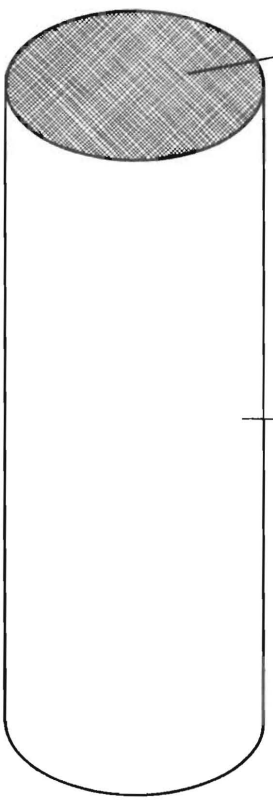


clear perforated p.v.c. sheet

p.v.c. soil pipe

p.v.c. strips hold bird protector on emergence cage

5 mm



terylene gauze to prevent hoppers escaping

Emergence Cage

p.v.c. soil pipe

Figure 4.6.2

Diagram of emergence cage.

Results from the fixed material are shown in Table 4.6.3. The eggs were placed at the stations in late autumn and removed at the end of the following summer. Therefore, they spent the winter, spring and summer at the selected station. At stations A, B, C and D the froth of the complete egg pods had broken down. With two exceptions the eggs had not developed past the diapause stage. The exceptions were three embryos of Brachaspis nivalis at station D which had entered blastokinesis, and all the B. collinus embryos at station A which were very close to hatching. The latter exception is important because eggs from this pod were placed at each location, yet developed only at Temple Basin.

Some as yet unidentified factor (or factors) in the alpine environment caused diapause termination in the Brachaspis collinus eggs at station A, presumably during the winter. (Examination of eggs from the same pod, from stations C and E, showed that they had not started post-diapause development when placed at the stations.) Post-diapause development would not start until the ground had warmed to above developmental zero for the eggs. Meltwater would prevent this occurring until the thaw had been essentially completed (Holway and Ward, 1963). Development from diapause stage to the stage where they were nearly ready to hatch took about three months.

The two pods of Sigaus villosus eggs laid in the laboratory, like those of the other species examined, went into diapause.

There is no evidence that diapause can occur at any stage

Table 4.6.3: Development of eggs at selected stations.

Species and Date Laid	Station*	Egg development
Brachaspis nivalis		
2.3.69 (whole pod)	A	Pod structure broken down. Eggs rotten.
1.3.69 (whole pod)	B	Not recovered.
10.1.69a	C	Embryos in diapause.
10.1.69a	E	Embryos in diapause.
10.1.69b (whole pod)	D)	Egg pod broken down.
	)	5 embryos at diapause.
21.2.69	D)	3 embryos had broken diapause and started to turn. Not possible to separate eggs of these two pods.
21.2.69	E	Embryos in diapause.
Brachaspis collinus		
16.1.69	A	Embryos very close to hatching.
16.1.69	C	Embryos in diapause.
16.1.69	E	Embryos in diapause.
21.1.69	B	2 embryos at diapause. 3 eggs had failed to develop.
21.1.69	E	Embryos in diapause

* See text for description of stations.

other than the end of anatrepsis, but it is possible that some eggs may require more than one period of cold treatment before diapause is terminated. This would not be unusual; Kreasy (1960) found that the eggs of one North American high altitude grasshopper species required a three year (three winter) developmental period, and those of another species required a two year developmental period. Similarly, there is no evidence that any eggs hatched without going into diapause, or that eggs laid early in the season hatch before the following winter. All the eggs examined went into diapause, irrespective of when they were laid.

The results of studies on the egg development of Brachaspis collinus, B. nivalis, Paprides nitidus and Sigaus australis can be summarized as follows:

1) Eggs go into an obligatory diapause.
2) Diapause occurs at the end of anatrepsis. Diapause embryos have dark eyes.
3) A period of cold treatment is required to terminate diapause.
4) The required period of cold treatment probably varies between pods and between species.
5) Rate of pre-diapause and post-diapause development is a function of temperature and varies with species. Brachaspis nivalis showed the most rapid development.
6) Some eggs, after a long period of time, are able to terminate diapause without a period of cold treatment.
7) Eggs can withstand a period of freezing during post-diapause development.

4.7 Proposed Life Cycle

The proposed life cycle of the New Zealand alpine grasshoppers can now be described on the basis of the preceeding evidence. Brachaspis collinus, Brachaspis nivalis, Paprides nitidus and Sigaus australis all appear to have similar life cycles. Data on Sigaus villosus, however, are insufficient to determine if this species follows the same pattern as the others.

Eggs may be laid at any time during the snow-free season. Given suitable temperatures the embryos develop till the end of anatrepsis when they all go into an obligatory diapause, which requires at least one period of winter cold for termination. It is possible that eggs laid in the field may, because of unsuitable temperatures, pass their first winter not in diapause, but rather in a state of quiescence. Following winter these eggs would resume developing until they went into diapause. After termination of diapause, post-diapause development proceeds, when temperatures permit, until hatching occurs. The nymphs that hatch develop through a specific number of instars according to species (see Hudson, 1970), until the adult stage is reached. Development is temporarily halted by winter and by periods of cold which can be passed by all stages in a state of quiescence. The adults mate, the female oviposits, and the cycle starts again. With the approach of winter adult females may go into a reproductive diapause, or may continue producing eggs. Death of

adult females is probably ultimately due to starvation during a cold period through lack of food reserves (fat body) which have been used during egg production.

The length of the grasshoppers' life cycle is unknown, but Batcheler (1967) considered that Brachaspis collinus at Cupola Basin did not reach maturity until about three years after hatching. This estimate seems reasonable to this author. Development is not tied to the seasons. The length of an individual life cycle will depend upon the temperatures in the habitat, which are a function of both altitude and local weather conditions.

The life cycles of the New Zealand alpine grasshoppers are, as stated by Batcheler (1967), "unusually flexible". The basis of this flexibility appears to be in the tolerance of all stages to winter cold. In view of this cold tolerance the possession of an obligatory diapause in the egg stage is surprising, especially as winter diapause is uncommon in New Zealand insects (Dumbleton, 1967). The possible origin of this diapause is discussed in Section 6.

Life cycles, similar to those proposed above, except for the egg diapause, have been suggested by Sutherland (1964) for the alpine weta (Hemideina maori), and proposed by Gibbs (1970) for the black mountain ringlet butterfly (Percnodaimon pluto). The life cycles of New Zealand alpine grasshoppers and Northern Hemisphere alpine grasshoppers are compared in Section 6.

Section 5

PARASITES AND PREDATORS

5.1 Parasites

There are only two published references to parasites in or on New Zealand alpine grasshoppers. Batcheler (1967) recorded the parasitism of Brachaspis collinus at Cupola Basin by red external mites, and Marples (1962) stated that grasshoppers were an important host of gordian worm larvae. The latter were not found in the alpine grasshoppers of Canterbury, but red external mites, which have been widely observed on the New Zealand grasshoppers, appear to be an important parasite. Five parasitic species were found on, or in, juvenile and/or adult grasshoppers. One egg parasite was discovered.

For each parasitic organism an attempt was made to establish the site and nature of parasitism, appearance and taxonomic status of the parasite, regional and seasonal variation in incidence of parasitism, preferred instar and sex of the grasshopper host, contagiousness of the parasite under laboratory conditions, and the effect of the parasite on its host.

Data from the additional specimens (Section 1.7) are included in this section. The terms "field grasshoppers" and "laboratory grasshoppers" will be used as defined in Section 1.8.

5.2 Mermithids (Nematoda)

Mermithids are frequently mentioned in the literature as parasites of grasshoppers (Uvarov, 1928; Cobb, Steiner and Christie, 1923; Rubtzov, 1934; Baylis, 1944; Stevanovic, 1961 and Blackith, 1968). Compared with the results of studies reviewed by Uvarov (1928), and described by Cobb, Steiner and Christie (1923), Baylis (1944), Crowcroft (1948) and Stabler (1952), the mermithids examined in this study were large and their incidence as parasites did not appear to change throughout the snow-free season.

Mermithids ranging in length from 5.5 to 400mm, were found in the body cavities of many grasshoppers (Fig 5.2.1). Usually only one or two (if any) of these nematodes were carried by grasshoppers taken from the field, but one laboratory specimen contained 49.

Only one mermithid was observed that emerged from a grasshopper in the laboratory. It was 190mm long, had a colourless, transparent, outer sheath surrounding an opaque white internal region, and showed no development of reproductive organs. It moved when placed in water, but made no apparent response to light.

In fixed specimens the transparent outer sheath and the opaque internal region were both coloured a light brown. None of the specimens examined showed any development of reproductive

Figure 5.2.1

Parasitic mermithid in the thoracic-abdominal cavity of a *Brachaspis collinus* adult male.

organs.

Mermithids were usually confined to the thoracic-abdominal cavity, but were occasionally present in the head, labium or legs. In adult grasshoppers, mermithids often seemed to have inhibited the development, or to have caused the atrophy of the host's reproductive organs.

Roundworms belonging to the phyla Nematoda and Nematomorpha are parasites of insects. Only nematodes of the family Mermithidae and gordian worms (Nematomorpha) attain the size of the worms examined without development of reproductive organs. Concern was expressed by Uvarov (1928) about differentiation of the superficially similar mermithids and gordians by many workers. The worms were identified as mermithids for the following reasons:

1) All the worms examined had smooth cuticles; whereas gordians characteristically have sculptured cuticles.
2) None of the worms examined had an anus; whereas gordians have an anus.
3) Mounted specimens showed a nematode-like structure of the anterior end and possessed a feeding stylet; whereas this type of structure is not found in gordians.
4) None of the worms examined had forked tails, which are characteristic of many male gordians.

The worms all appeared to be very similar, and although only a few were mounted and closely examined it can probably be safely stated that they were all mermithids. No gordian worms were found.

The worms bore some resemblance to Mermis nigrescens as described by Baylis (1944); but, because of the difficulties of mermithid taxonomy, no attempt was made to identify them beyond the family level.

In the usual life cycle of a mermithid the young larva, ingested by the host insect as an egg or larva (depending on species), burrows through the gut into the thoracic cavity and there increases rapidly in size. The parasitic stage of the life cycle is terminated when the worm leaves the host through the mouth, anus or body wall and then burrows into the soil, where development to maturity proceeds.

Data from laboratory grasshoppers were not included in the following discussion. The mermithid life cycle shows they would not be contagious between grasshoppers in the laboratory. Evidence suggested, however, that the parasite could be contracted in the laboratory, presumably from food plants. Laboratory grasshoppers had a higher percentage of parasitism than field grasshoppers and only laboratory grasshoppers contained very large numbers of very small nematodes.

The incidence of parasitism did not appear to be seasonal. Parasitised animals were found from October to April, and there was no relationship between the size of worm and the date the host was caught.

Although mermithid parasites were found in all grasshopper species studied, they were observed in field collected specimens

only at the Temple Basin and Porter Heights study areas, and in a specimen of Paprides nitidus from Mt. Bruce, Bealey. In all cases the percentage of parasitism was low (Table 5.2.1).

Table 5.2.1: Incidence of mermithid parasites in field grasshoppers of all ages.

Species and Study Area	N	P	%
Brachaspis collinus			
Temple Basin	309	1	0.32
Brachaspis nivalis			
Craigieburn	28	0	0
Porter Heights	97	4	4.12
Paprides nitidus			
Craigieburn	33	0	0
Porter Heights	83	2	2.41
Temple Basin	53	0	0
Sigaus australis			
Craigieburn	7	0	0
Porter Heights	109	8	7.34
Sigaus villosus			
Craigieburn	0	-	-
Porter Heights	17	1	5.88

N = number of grasshoppers examined

P = number of grasshoppers parasitised by mermithids

% = percentage of grasshoppers parasitised by mermithids

Parasitism by mermithids did not appear to be confined to any particular instar or sex. The youngest parasitised grasshopper was an instar II male of Brachaspis collinus.

The incidence of parasitism by mermithids appears to be low. However, the reliability of the figures in Table 5.2.1 as an estimate of the occurrence of the parasite in the field is difficult to determine without greater knowledge of the biology of the worm. For this reason the incidence of parasitism may not be higher at Porter Heights, as the figures in the table imply.

As stated previously, parasitism by mermithids seems to affect the development of the gonads of grasshoppers. The relatively large bulk of the parasite may interfere with normal developmental processes in the host. Thus it would be expected that parasitism by a mermithid would be harmful to a grasshopper. Reports in the literature state that grasshoppers usually die very soon after the mermithid has left them.

5.3 External Mites

Red mites (Fig 5.3.1) were frequently found parasitising grasshoppers. The mites were always attached by their mouthparts, usually to the tympanum, wings or the underside of the elytra. One mite was found attached to the epiproct of a

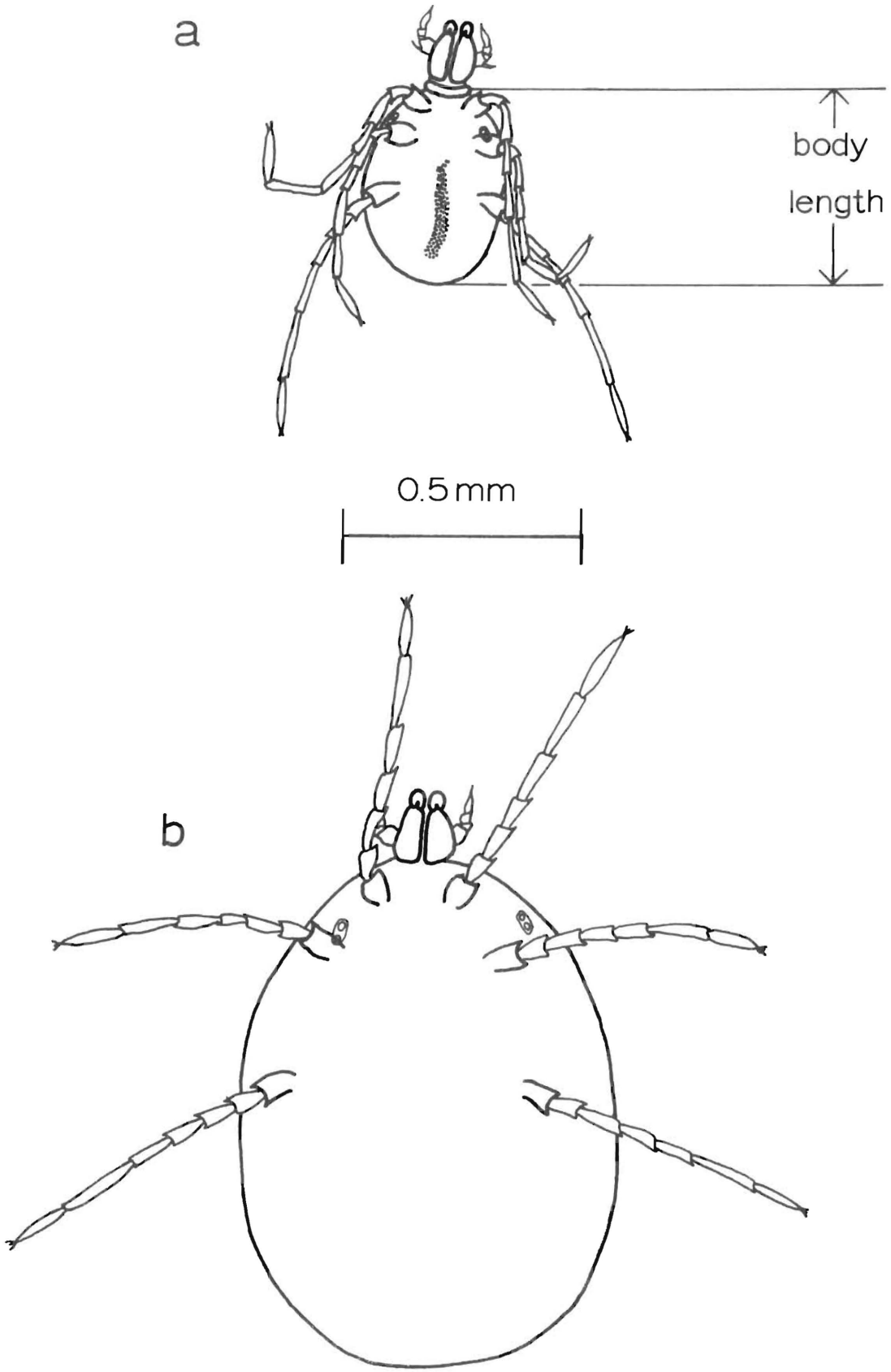

a
body
length
0.5 mm
b

Figure 5.3.1

(a) A small specimen of erythraeid mite (setation and claws not shown) from Brachaspis nivalis instar I male. (b) Large specimen of erythraeid mite from a Brachaspis nivalis instar IV female.

Brachaspis nivalis instar IV female and some were attached to the thorax or abdomen of some first instar grasshoppers. Their body length ranged from 0.36 mm to 1.08 mm (body length being measured as shown in Fig 5.3.1(a)). Their concentration ranged from one to 25 mites per host grasshopper with the majority of hosts carrying one to three mites.

Based on the shape and setation of the scutellum, form and position of the eyes, and the general appearance of the cuticular striations, all the mites examined appeared to belong to the same species. All the mites bore only three pairs of legs. They were classified according to Baker and Wharton (1952) as belonging to either family Erythraeidae or family Smarididae (Acarina: Trombidiformes) and were considered to be larvae. Dr. Rowan Emperson of Lincoln College, Canterbury, New Zealand (pers. com.) was of the opinion that all the specimens he examined belonged to the same species and he tentatively placed them in the family Erythraeidae and the genus Erythrites Southcott, 1961.

As with many parasites, a major problem in the taxonomy of erythraeids is the establishment of relationships between adults and larvae. Dr. Emperson is hoping to rear these mites through to adults so that a positive identification can be made.

Parasitism of acridids by erythraeids is well known and has been recorded in New Zealand by Batcheler (1967), and in other countries by Uvarov (1928), Rubtzov (1934), Lawrence (1940a, 1940b) and Richards and Waloff (1954). The taxonomy of the

Erythraeidae and the closely related Smarididae was reviewed by Southcott (1961).

Adult erythraeids lay eggs that hatch to give larvae which attach to suitable insect intermediate hosts as six-legged parasites. Mature larvae drop off their hosts and moult to form the eight-legged adults (Baker and Wharton, 1952).

Mites were found parasitising grasshoppers in the field from October through to April, and it would thus appear that their occurrence is not seasonal. There was, however, a slight increase in the incidence of parasitised animals towards the end of the snow-free season.

Of the 93 parasitised field grasshoppers 90.5% were adults, 4.3% instar VI, 1.1% instar IV and 4.3% instar I. The records suggest there may be a higher incidence of parasitism by external mites among adult females than among adult males. Table 5.3.1 shows the distribution of parasitism of field grasshoppers by external mites. The parasite has been observed on all the species studied, and has been found in all the study areas. In addition, external mites have been found on specimens of Paprides nitidus collected from Donald Hill, Glenariffe Station and from the Crawford Range. The table also shows that mites are less abundant on the scree-inhabiting grasshoppers Brachaspis nivalis and Sigaus villosus.

Table 5.3.1: Parasitism of field grasshoppers by external mites.

Species and Study Area	Adults N	Adults P	Adults %	All Stages N	All Stages P	All Stages %
Brachaspis collinus						
Temple Basin	156	45	28.85	309	50	16.18
Brachaspis nivalis						
Craigieburn	45	0	0	81	0	0
Porter Heights	50	0	0	97	2	2.06
Paprides nitidus						
Craigieburn	20	2	10.00	33	2	6.06
Porter Heights	38	8	21.05	83	9	10.84
Temple Basin	41	18	43.90	53	18	33.96
Sigaus australis						
Craigieburn	5	1	20.00	7	1	14.29
Porter Heights	53	8	15.09	109	9	8.26
Sigaus villosus						
Craigieburn	0	-	-	0	-	-
Porter Heights	13	2	15.38	17	2	11.76

N = number of grasshoppers examined

P = number of grasshoppers parasitised by external mites

% = percentage parasitism

Table 5.3.2 compares the parasitism by external mites on field and laboratory adult grasshoppers. In most cases the percentage parasitism was higher on the field grasshoppers.

Table 5.3.2: Comparison of parasitism by external mites of adult field and laboratory grasshoppers.

Species and Study Area	Field			Laboratory		
	N	P	%	N	P	%
Brachaspis collinus						
Temple Basin	156	45	28.85	368	34	9.24
Brachaspis nivalis						
Craigieburn	45	0	0	22	0	0
Porter Heights	50	0	0	50	0	0
Paprides nitidus						
Craigieburn	20	2	10.00	24	3	12.50
Porter Heights	38	8	21.05	69	4	5.80
Temple Basin	41	18	43.90	118	18	15.25
Sigaus australis						
Craigieburn	5	1	20.00	6	0	0
Porter Heights	53	8	15.09	52	5	9.62
Sigaus villosus						
Craigieburn	0	-	-	12	0	0
Porter Heights	13	2	15.38	22	4	18.18

N = number of grasshoppers examined
P = number of grasshoppers parasitised by external mites
% = percentage parasitism

The figures for incidence of parasitism by external mites may be an underestimate as a result of mites falling off their host while in preservative, but the number lost in this way should not be great because the mites were usually attached firmly by their mouthparts to protected parts of the host's body. It is therefore felt that the incidence figures cited give a realistic estimate of the incidence of parasitism in the animals collected. But, since little is known of the distribution of the mite in the field, it cannot be said that the results give an accurate estimate of the occurrence of parasitism by mites in the field. The lower incidence of parasitism on the scree inhabiting species suggests that the adult requires vegetated ground.

Batcheler (1967) observed similar mites parasitising Brachaspis collinus and Paprides nitidus at Cupola Basin. He recorded a much higher incidence of parasitism (a peak average of 11.8 mites per adult female Brachaspis collinus in March 1965) than was observed in this study, and he records peaks of parasitism occurring.

Parasitism by external mites does not appear to affect the grasshoppers adversely.

5.4 Tracheal Mites

This parasite occupies the airsacs and trachea of the thorax and abdomen of grasshoppers. When a parasitised animal is dissected the infection appears as a mass of discrete, small white globules (eggs) and larger orange globules (gravid females) in the air sacs. Often there is darkening of patches of the walls of the airsacs - probably a result of damage caused by the parasite feeding. In cases of very light parasitism the mites are not very obvious, but when parasitism is heavy the airsacs are bulging with mites. In heavily parasitised adult female grasshoppers the ovaries regress. These mites were not found on the outside of the grasshopper's body.

The mite was identified using Baker and Wharton (1952) as belonging to family Podapolipodidae (Acarina: Trombidiformes: Tarsonemini). It closely resembles Locustacarus trachealis Ewing. Locustacarus is placed in various families: Ewing (1924) places it in Tarsonemidae, Baker and Wharton (1952) in Podapolipodidae, and Regenfuss (1968) in Podapolipidae.

Locustacarus trachealis was the first tracheal mite found in grasshoppers. It was identified and described by Ewing (1924) and its biology was described by Wehrle and Welch (1925). The tracheal mite in the grasshoppers studied, like L. trachealis, has a very reduced life cycle. Larval development occurs in the egg and a six-legged adult hatches out. As it develops,

the region between the anterior two pairs of legs and the posterior pair of legs of the female mite increases enormously in size. The relative number of eggs and adult females in the air sacs and trachea of parasitised grasshoppers suggests that the female mites can lay very large numbers of eggs. All the life history stages of the mite can be found in the same host, and are illustrated in Fig 5.4.1.

The size of eggs in alcohol ranged from 0.149 to 0.163 mm in length and 0.106 to 0.114 mm in width; gravid females were 0.45 to 0.50 mm long. The egg sizes are similar to those measured by Wehrle and Welch for L. trachealis (0.140 to 0.169 mm in length by 0.092 to 0.118 mm in width). The tracheal mite studied here differs from L. trachealis in that it occurs in adult grasshoppers of both sexes while L. trachealis was only found in adult female grasshoppers. Microscopic examination showed that this mite possessed stylets similar to those of L. trachealis. Damage to the walls of the air sacs and trachea of parasitised grasshoppers suggest that the mite feeds in a similar way to L. trachealis, by puncturing the walls of the trachea and air sacs.

A second species of tracheal mite parasitising acridids, Locustacarus locustae, was described by Ewing (1932) (cited in Harris, 1940); its biology has been described by Harris (1940). L. locustae differs slightly from L. trachealis in structure, possibly lacks a male, and has been found on the outside of the grasshopper it infects (Locusta migratoria migratorioides).

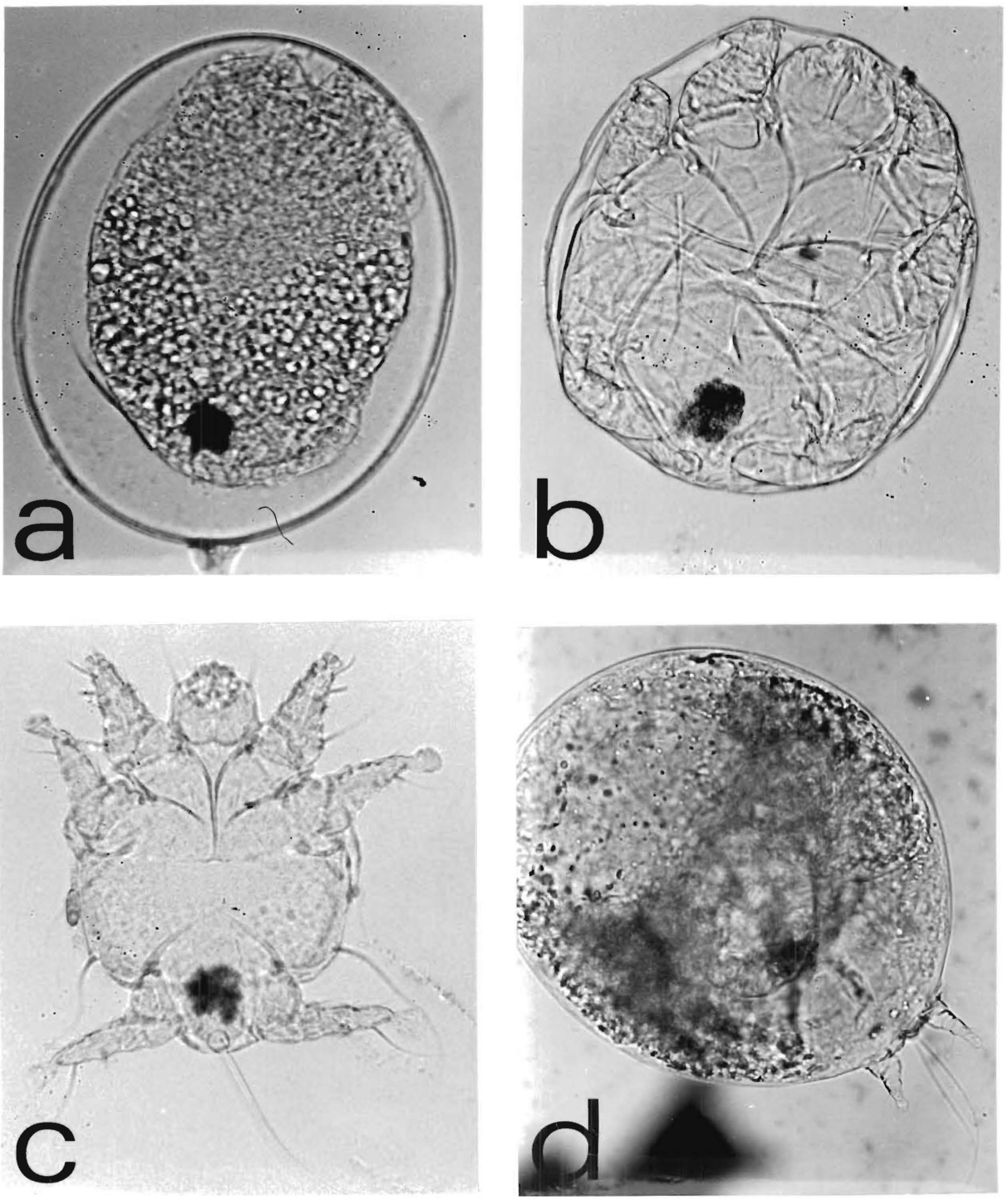

a
b
c
d

Figure 5.4.1

Stages in the life cycle of the tracheal mite. (a) Egg. (b) Egg about to hatch. (c) Non-gravid adult female. (d) Gravid female.

In size, L. locustae is slightly larger than both L. trachealis and the mite found in this study. Harris does not state whether L. locustae was restricted to a particular sex or instar of the host.

Regenfuss (1968), in his review of the family Podapolipidae, mentions a third species of Locustacarus parasitising acridids - L. solitarius (Lavoipierre, 1941). In his 1941 paper Lavoipierre describes this mite as Podapolipus solitarius, but unfortunately gives no information on its biology. Lawrence (1940b) mentions the genus Locustacarus among the mites parasitising Locusta migratoria migratorioides.

Grasshoppers parasitised by tracheal mites were found from October to May, but results suggest an increase in the incidence of parasitism towards the end of the snow-free season.

In laboratory grasshoppers the parasite has been found in adults of both sexes, in females of instars IIIA, IIIB, V and VI, and in males of instars IV and VI. In field grasshoppers, however, the parasite has been found only in adults (of both sexes). Because laboratory incidence differs from that in the field, the data presented in Table 5.4.1 and 5.4.2 are from field grasshoppers only. In addition to the data in Table 5.4.1, mites have been found parasitising specimens of Paprides nitidus and Brachaspis nivalis from Porters Pass, Paprides nitidus and Brachaspis collinus from Amuri Ski Field, Sigaus australis from Donald Hill, Glenariffe Station and Paprides nitidus and Sigaus

Table 5.4.1: Incidence of parasitism by tracheal mites in adult field grasshoppers.

Species and Study Area	N	P	%
Brachaspis collinus			
Temple Basin	156	0	0
Brachaspis nivalis			
Craigieburn	45	0	0
Porter Heights	50	19	38.00
Paprides nitidus			
Craigieburn	20	0	0
Porter Heights	38	16	42.11
Temple Basin	41	2	4.88
Sigaus australis			
Craigieburn	5	0	0
Porter Heights	53	13	24.53
Sigaus villosus			
Craigieburn	0	-	-
Porter Heights	13	0	0

Table 5.4.2: Comparison of the incidence of parasitism by tracheal mites in adult male and female field grasshoppers.

Species and Study Area	Males			Females		
	N	P	%	N	P	%
Brachaspis nivalis						
Porter Heights	22	14	63.64	28	5	17.86
Paprides nitidus						
Porter Heights	19	12	63.16	19	4	21.05
Temple Basin	11	2	18.18	30	0	0
Sigaus australis						
Porter Heights	15	8	53.33	38	5	13.16

N = number of grasshoppers examined
P = number of grasshoppers parasitised by tracheal mites
% = percentage of grasshoppers parasitised by tracheal mites

australis from the saddle between Lake Clearwater and the Rangitata River. Tracheal mites have thus been found in all the species studied except Sigaus villosus. No parasitised animals were found at Craigieburn and the incidence of parasitism at Temple Basin was small.

Table 5.4.2 compares the incidence of tracheal mites in male and female adult field grasshoppers. In all cases the percentage parasitism of the males is much higher than that of the females.

The restriction of the parasite to adult grasshoppers in the field and its more widespread distribution among the developmental stages of grasshoppers kept in the laboratory suggests (1) that grasshoppers can be infected by the parasite in the laboratory and (2) that infection is probably passed on by bodily contact. In the field, grasshoppers would rarely come into contact with each other except during copulation, while in the artificial conditions of the laboratory grasshoppers of all instars are forced into close contact with one another. A consideration of the life history stages of the mite (Fig 5.4.1) would suggest that the stage best equipped to pass on the infection would be the non-gravid female. This is supported by the evidence of Fig 5.4.2 which shows three non-gravid females (or males) in a length of narrow trachea. They could only have reached this position if they were capable of movement or had been drawn there by respiratory movements. Respiratory movements

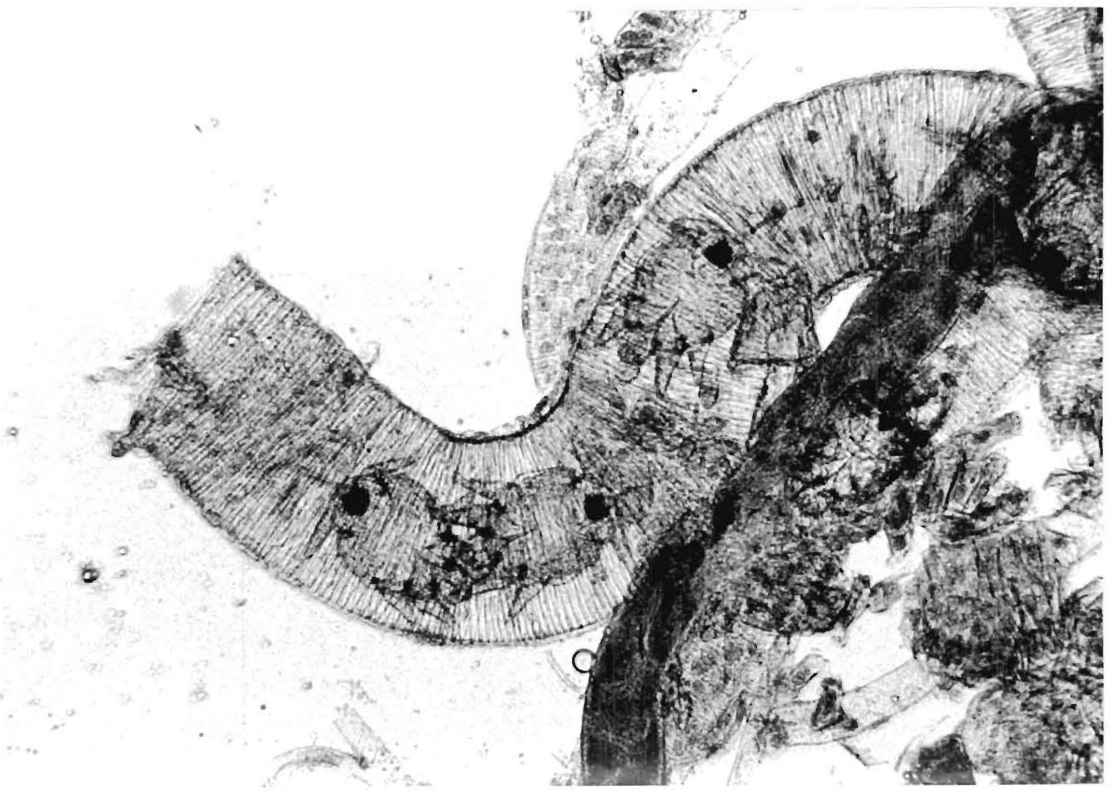


Figure 5.4.2

Section of grasshopper narrow trachea containing adult tracheal mites.

should also shift eggs, which are approximately the same size as non-gravid adults and appear to be just as free in the air sacs. As no eggs were found in this length of trachea, it would appear that adult non-gravid mites are capable of movement and are the most likely infective stage.

In cases of light infection the mite may have little effect on its host grasshopper. But with heavy infections the thoracic and abdominal air sacs are packed with mites, and in some heavily infected females the ovaries are undeveloped. It thus appears likely that heavy infections have harmful effects on the hosts. Bailey and Lee (1959) reached a similar conclusion from their studies of Acarapis woodi, a tracheal parasite of bees (Isle-of-Wight disease).

Tracheal mites, like the mermithids and external mites, are present throughout the snow-free season. The apparently greater abundance of mites observed at the eastern edge of the alpine chain could be due to (1) a preference for the climatic conditions in this region, (2) recent arrival of the parasites in New Zealand, or (3) cycles of greater or lesser abundance which are out of phase in different regions. Which (if any) of these conditions may account for the apparent distribution of the mites cannot be established on presently available evidence.

5.5 Cestodes

Four specimens of Brachaspis nivalis (2 adult males, 1 adult female and 1 sixth instar female) collected at Craigieburn in December 1966, February 1968 and February 1969 were found on dissection to contain off-white, opaque discs 0.6 mm to 0.8 mm in diameter attached to the intestine (and among the ovarioles in the adult female). On further examination these were found to be cestode cysticercoids (Fig 5.5.1). The cysticercoids bear two circles of well formed hooks, each circle containing the same number of hooks and with a second circle slightly below and between the hooks of the first. The hooks were counted on two specimens - the first had 16 and the second 18 hooks per circle. Four suckers were identified.

The host of the adult of this cestode species is unknown. An insect-eating bird might be a logical primary host, and the pipit a likely bird. Four pipits were taken, three of which had cestodes in their intestine. Whether or not these were of the same species as the cysticercoids in the grasshoppers could not be established.

No reference to cestodes parasitising grasshoppers was found in the literature.

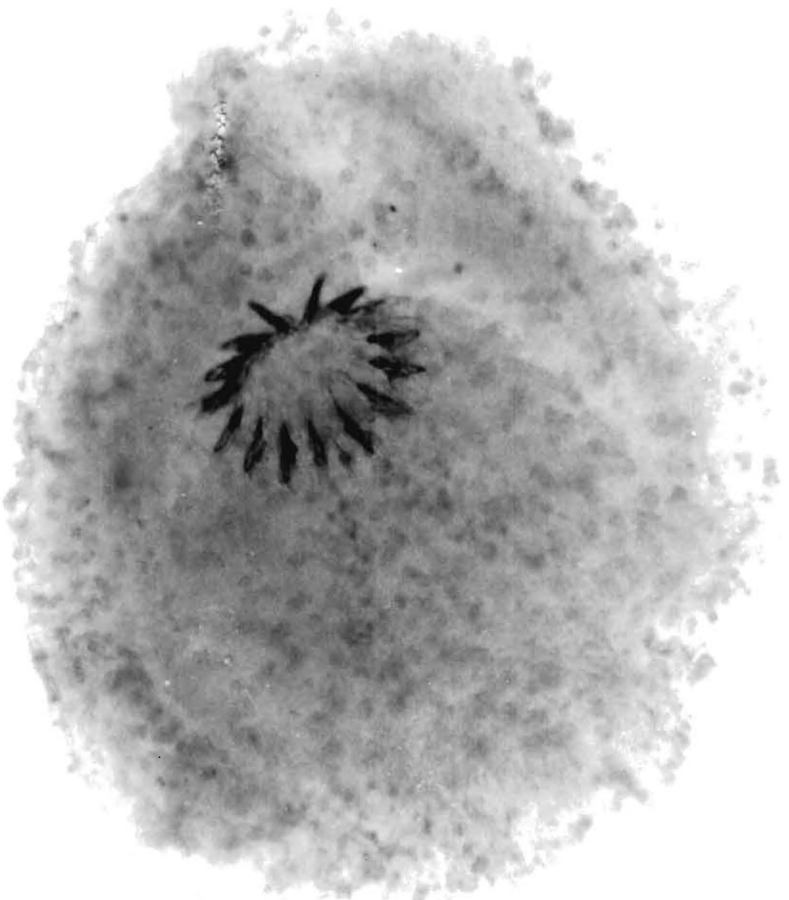


Figure 5.5.1

Cysticercoid from Brachaspis nivalis adult female.

5.6 Egg Parasite

Despite the scarcity of eggs collected from the field, one egg parasite was found. Small hymenoptera, placed in the family Scelionidae, emerged from field collected eggs of Brachaspis collinus. Dr. Lubomir Masner of the Institute of Entomology, Czechoslovak Academy of Sciences, Praha, Czechoslovakia (pers. comm.), placed these specimens in the genus Scelio, but could not be more specific.

The genus Scelio is well known as a parasite of grasshopper eggs and the relevant literature has been reviewed by Uvarov (1928) and Greathead (1963).

5.7 Gregarines

Many of the grasshoppers dissected were observed to be parasitised by gregarine protozoans (Class Sporozoa). These were found in the gastric caecae and between the wall of the midgut and the peritrophic membrane.

5.8 Discussion

Except for the cestode cysticercoids, the parasites found

are not unusual. The absence of dipteran parasites, however, and the lack of seasonal distribution of the parasites, are unusual.

Most of the literature on grasshopper parasites reports that dipteran parasites are abundant and are often the most important parasites of grasshoppers (see reviews by Uvarov, 1928; and Greathead, 1963). No dipteran parasites were identified during this study. If they had been present it is very likely that they would have been discovered. Dugdale (1969) has shown that tachinids with larvae parasitic in coleoptera are present in the general habitat of the New Zealand alpine grasshoppers.

Apart from some evidence of an increase in incidence of parasitism towards the end of the snow-free season, none of the parasites studied showed a definite seasonal distribution. As a similar conclusion was drawn concerning the seasonal incidence of instars in the grasshoppers (Section 4.2), it can be concluded that those parasites for which sufficient evidence is available have adapted to the life cycle of their hosts and have become essentially independent of season during the snow-free period.

5.9 Predators

The cryptic colouration of the grasshoppers would suggest that they have been and are subject to selection pressure from a

diurnal, visual-image-forming predator. The most obvious potential predators in this category would be birds. The birds observed in the study areas were the pipit (Anthus novaeseelandiae novaeseelandiae), black-backed gull (Larus dominicanus), New Zealand falcon (Falco novaeseelandiae), kea (Nestor notabilis) and the hawk (Circus approximans). The rockwren (Xenicus gilviventris gilviventris) was not observed by the author, but has been by many other people.

A permit was obtained from the Internal Affairs Department to take pipits and black-backed gulls. Twelve pipits were shot but no black-backed gulls were obtained. Five of the pipits were found to contain grasshopper remains. Examination of the disgorged crop contents of one kea revealed no insect remains, and Jackson (1960) in his work on keas at Arthurs Pass found no evidence that keas were eating grasshoppers. Redhead (1969) found that the percentage of insects eaten by harrier hawks was very low. Falcons were infrequent visitors to the study area. The most important bird predators are probably the pipit and perhaps the rockwren.

Carroll (1963) found that 13 out of 86 specimens of the North Island weka (Gallirallus greyi) contained grasshoppers. Although this species does not occupy alpine regions, the buff weka (Gallirallus hectori) was formerly very common in the tussock grasslands on the eastern side of the Southern Alps. This species is now limited in distribution and is not present in the

study areas, but it has possibly been an important predator in the past. Similarly, the chukar partridge, although not present in the study areas, could be a potential grasshopper predator. Williams (1950) stated that their altitudinal range extends up to the permanent snowline in summer. Marples and Gurr (1953) record the presence of grasshoppers in the crop contents of chukar in New Zealand, and Weaver and Haskell (1967) found animal matter, chiefly grasshoppers, constituted 11% of the autumn diet of chukar in Nevada (U.S.A.).

Three other vertebrates occur in the study areas which would be potential predators: the gecko (Hoplodactylus), the mouse (Mus musculus) and the stoat (Mustela erminea). Khonyakina (1965) found that in the U.S.S.R. grasshoppers make up a small part of the diet of lizards. Richards and Waloff (1954) showed that the field mouse (Apodemus sylvaticus sylvaticus) readily fed on grasshoppers nymphs in cages, but were unable to say if they did so in the field. Fitzgerald (1964) showed that stoats from bush areas ate large numbers of wetas and some cockroaches. It would thus seem possible that those stoats in alpine tussock areas would eat grasshoppers.

Among animals belonging to other phyla, insects and spiders must be considered as potential predators; particularly on grasshopper eggs and young nymphs. Older grasshoppers are quite large compared to the other invertebrates in the environment and are probably not greatly affected by them. Insect predators of

grasshoppers are discussed by Dempster (1963), Greathead (1963) and Uvarov (1928).

Section 6

EVOLUTION AND ADAPTATION OF NEW ZEALAND ALPINE GRASSHOPPERS TO THEIR ENVIRONMENT

The New Zealand grasshopper fauna is unique because it contains a very high proportion of alpine species. Bigelow (1967) described 15 species of grasshoppers in New Zealand of which 12 are alpine. Two of the lowland species (Locusta migratoria L. and Phaulacridium marginale (Walker)) are not endemic to New Zealand, and were probably post-Pleistocene immigrants. The remaining 13 species are endemic to New Zealand and all but one (Sigaus campestris (Hutton)) are restricted to alpine areas. These alpine grasshoppers display many characteristics in their morphology, behaviour and life cycles which make them well adapted to their environment.

Mani (1968), in his review of the ecology and biogeography of high altitude insects, devoted considerable space to general considerations of the high altitude environment and ecological specializations of high altitude insects. Although Mani's definition of high altitude insects as "an ecologically highly specialized, mountain autochthonous group existing exclusively in the biome above the forest, at elevations above 2000-2500 m" excludes the New Zealand alpine grasshoppers (they descend much lower than 2000 m), his discussion of the high altitude environment does have some applicability to the New Zealand alpine regions. Mani considered that the principle factor distinguishing the high from the low altitude environment is the difference in atmospheric pressure. However, it is the manifestations of this difference which are important to the high altitude insects.

Because of the reduced atmospheric pressure the air at high altitudes has high transparency; consequently, the high altitude environment receives high concentrations of ultra-violet radiation, has a high rate of insolation and radiation resulting in large diurnal fluctuations in temperature, has a low atmospheric temperature resulting in snow and tends to be arid. High altitude areas are frequently subjected to more wind and higher wind speeds than the nearby lowlands.

Air pressure as such is not important to insects. Lutz (1929) described experiments which showed that insects were extremely tolerant of low air pressure, and Uvarov (1931) stated that insects "are able to tolerate enormous fluctuations in pressure, such as can never occur under natural conditions". The effect of high concentrations of ultra-violet radiation on insects is unknown. Most investigations using ultra-violet light have dealt with the effect of much higher than normal concentrations, but Caldwell (1968) concluded, from field experiments, that ultra-violet radiation was not a very important factor for alpine plants. Because insects are poikilotherms, the large diurnal temperature fluctuations, the low atmospheric temperatures and the winter cold are important factors in the high altitude environment. It is perhaps to these factors that insects make the greatest adaptations. The New Zealand mountains are subject to arid periods, but overall aridity is tempered by the high precipitation associated with an oceanic climate. The

large amount of wind in the alpine environment could be an important factor for the insect residents. Many high altitude winged insects have the habit of flying just above the surface of the ground, which is probably a behavioural adaptation that protects them from being blown out of their habitat by strong winds. Reduction or loss of wings is more common among high altitude insects than among those living at low altitudes.

The major adaptations of the New Zealand alpine grasshoppers are to the cold in their environment. They are all diurnal in behaviour and their activity depends on their bodies being warmed by radiant energy from the sun. The grasshoppers commence and conclude their daily activities sitting, often on rocks, with their bodies aligned at right angles to the incident rays from the sun. Compared with Locusta migratoria (as a typical lowland grasshopper) the New Zealand alpine grasshoppers have a much thicker and more highly pigmented exocuticle. The heavy pigmentation would aid in the rapid absorption of radiant energy and, in addition, would confer protection against ultra-violet radiation. All species, including the lowland species Sigaus campestris, have very reduced wings. The two scree inhabiting species (Brachaspis nivalis and Sigaus villosus) bear extensive external setation which could insulate them against heat loss. The setation was most dense on S. villosus, which also occupied the highest altitudinal range of any of the species studied. In addition, S. villosus bears a protruding frons, a character which

was considered by Mani (1968) to be a structural adaptation to increase the area of an insect available for heat absorption and to act as a heat sensor.

The New Zealand alpine grasshoppers could not be reared in the laboratory or under outdoor conditions at low altitude. As they obviously live successfully in alpine areas this would suggest that their physiology has evolved so that it can function satisfactorily only in an alpine or subalpine environment.

The adaptations described above could be found among insects in most alpine communities throughout the world. The life histories of the New Zealand alpine grasshoppers, however, differ from those of the Northern Hemisphere alpine grasshoppers. The life cycles of alpine grasshoppers are a means of overcoming the limitations of, and consequently are adaptations to, their alpine environment. Because insects are poikilotherms their metabolic rate is proportional to temperature, and thus inversely proportional to altitude. Therefore, metabolic rate and growth rate would decrease with altitude.

The New Zealand alpine grasshoppers have adapted to the alpine environment by becoming cold tolerant. There is an obligatory diapause in the egg stage which is terminated by a period of winter cold, but subsequent development from hatching to maturity probably takes two to four years and overwintering may occur in any stage including the egg and adult. Depending on sex and species, the number of juvenile instars varies from

five to seven (Table 1.5.1) which is equal to or greater than the usual five or six instars in the Catantopinae (Ramsay, 1964). Bigelow (1967) and Staples (1967) have shown that the size of some species of New Zealand alpine grasshoppers increases with altitude, and the largest species studied (Sigaus villosus) is restricted to the highest altitudinal range. As growth rate would be slower at higher altitudes it would be expected that S. villosus would take the longest time to develop and would have the longest life cycle of the New Zealand grasshoppers. This is in accord with Uvarov (1931), who stated that development at low temperatures produces larger insects and that the individual lives of insects become longer at lower temperatures.

The presence of a diapause in the egg stage distinguishes the alpine grasshoppers from the majority of New Zealand insects. Dumbleton (1967) states "New Zealand insects most commonly pass the winter in a prolonged larval or nymphal stage..." and winter diapause "... is not pronounced in the alpine and subalpine faunas where it might be expected to be most common." The alpine grasshoppers are able to overwinter in the larval and adult stages. They are clearly able to overwinter without diapause, yet they possess a winter diapause in the egg stage. It is, therefore, hypothesized that the egg diapause of the New Zealand alpine grasshoppers evolved independently from the rest of the life cycle as it now exists. The egg diapause will be discussed later in this section.

Most Northern Hemisphere alpine grasshoppers have an "abbreviated" life cycle. Eggs overwinter in diapause and the grasshoppers hatch, develop to maturity, oviposit and die in one season (Alexander and Hilliard, 1964 and 1969; Stevanovic, 1961; and Dreux, 1961). As altitude increases the growing season effectively shortens because air temperatures are lower and the snow-free season may be shorter. Therefore, high altitude grasshoppers have to complete their development quickly. This can be achieved by decreasing the number of juvenile instars (Aeropedellus clavatus in North America has only four juvenile instars in each sex - Alexander and Hilliard, 1964), and/or by decreasing the size at which maturity is reached (six measurements made on grasshoppers from the Colorado Front Range by Van Horn, 1965, were found to decrease in size with increasing altitude). These adaptations are the opposite of what has been observed in New Zealand.

Some Northern Hemisphere species do have life cycles longer than one year if juveniles are able to overwinter or if eggs require more than one winter's cold to terminate diapause (Criddle cited in Alexander and Hilliard, 1969; Alexander and Hilliard, 1964; Alexander, 1967; Kreasy, 1960; and Pickford, 1953). Such records are not extensive, but Uvarov (1966b) suggested that more acridids may overwinter as adults or larvae than is generally believed.

Comparison of the two life cycle types shows that the New

Zealand alpine grasshoppers have adapted to their environment by becoming tolerant to the cold at all stages, while the Northern Hemisphere alpine grasshoppers have adapted to their environment by abbreviating their life cycles so only one or two stages are exposed to the winter cold. The basic difference between the two types of life cycle is the toleration of winter cold by the grasshoppers. This would suggest either that New Zealand alpine grasshoppers are more resistant to the cold than Northern Hemisphere alpine grasshoppers, or that the New Zealand alpine climate is, and was, milder than that in the Northern Hemisphere.

No comparative tests have been made of the cold resistance of New Zealand and Northern Hemisphere grasshoppers, but Cockayne (1958) records that many New Zealand alpine plants could not endure the winter temperatures at Kew (Great Britain), hardly any the winter temperatures of Berlin, and that a period of almost constant frost at Queenstown in 1923 killed many supposedly hardy plants. Dumbleton (1967) has noted that the tolerance to winter cold of the majority of the New Zealand insects is paralleled by a lack of winter deciduousness in New Zealand plants. This would suggest that insects and plants may have a similar tolerance for winter cold. If this is so, the examples of Cockayne, although not showing that the New Zealand alpine grasshoppers are any more or less cold tolerant than those from the Northern Hemisphere, would suggest very strongly that the winter cold in the Northern Hemisphere is much more severe than that in New Zealand, thus

preventing overwintering of most stages.

This view is reinforced by a comparison of air temperatures from alpine regions in the Northern Hemisphere and New Zealand (Table 6.1). These suggest that winter temperatures are higher in the Southern Hemisphere alpine areas. As snow cover would insulate the alpine habitat of the grasshoppers from the air temperature and maintain it at approximately $0^{\circ}C$ the important period must be before the snow falls. Morris (1965), comparing the climate in the Craigieburn Range with that in mountain regions in the Northern Hemisphere, noted that the one markedly dissimilar factor was the winter minimum. He attributed the milder winter climate of New Zealand to the oceanic influence.

The life cycles of New Zealand and Northern Hemisphere grasshoppers probably evolved originally during the Pleistocene cold climate. The New Zealand alpine grasshoppers are considered to have been in New Zealand prior to the Pleistocene, and to have survived the Pleistocene cold climate in this country (Bigelow, 1967; Irving, 1967; and Peterson, 1968). It has been hypothesized by Dumbleton (1967) that the Pleistocene cold climate in New Zealand was not as severe as that in the Northern Hemisphere. He considers this is why insects that can only over winter in diapause are common in the Northern Hemisphere and uncommon in New Zealand. This difference in intensity of Pleistocene cold climates could explain the difference that exists between the life cycles of the alpine grasshoppers from the

Table 6.1: Comparison of the mean monthly air temperatures of three Northern Hemisphere and two New Zealand mountain areas. (Temperature is given in degrees Celsius).

	Southern Hemisphere Months											
Site and Source	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Otz Valley, Austria. Station at treeline. (Aulitzky, 1968)	9.0	9.3	7.7	3.0	-1.8	-4.7	-5.7	-4.7	-3.7	-1.0	3.3	7.3
Berthoud Pass, Colorado. Station just below upper limit of treeline at 11,315 ft. (Judson, 1965)x	10.6	8.9	5.0	0.6	-7.2	-11.1	-11.7	-11.1	-8.9	-4.4	2.8	6.7
Leadville, Colorado. Station 1500 ft below the treeline at 10,200 ft. (Wardle, 1965)x.	13.9	13.1	9.7	4.1	-3.0	-6.5	-8.1	-7.0	-4.8	0.5	5.6	10.6
Craigieburn (N.Z.). White Star station just above the treeline at 4500 ft. (Morris, 1965)x	11.1	10.0	8.9	6.1	3.9	1.1	-0.6	0	1.7	6.7	6.1	10.0
Foggy Peak Ridge. Station just above what would be the treeline at Porters Pass at 4500 ft. (Molloy, 1963)	12.0	16.0	10.0	6.0	0	-3.0	-2.0	-1.0	0	6.0	10.0	8.0
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
	Northern Hemisphere Months											

x = converted from degrees Fahrenheit

Northern Hemisphere and New Zealand.

Dumbleton (1967) noted that the incidence of diapause was very low in New Zealand insects. The present study has shown that the New Zealand alpine grasshoppers can overwinter in any stage and suggests that the grasshoppers, apart from the obligatory egg diapause, have similar life cycles to many other New Zealand insects. The similarity of their life cycle to that of other New Zealand insects would suggest that their egg diapause may be unecessary as an overwintering mechanism and probably did not evolve during the Pleistocene. As it is very doubtful that it would have evolved since the Pleistocene, it is suggested that it is a pre-Pleistocene character. If this is so, it would suggest that the alpine grasshoppers may have been primitively alpine with a life cycle similar to the present day Northern Hemisphere alpine grasshoppers. Other evidence also suggests that this may have been the case. Only one of the 13 endemic grasshopper species has descended to the lowland. This shows a very low rate of invasion of a lowland - which appears to carry very little in the way of direct competitors - by a group that has speciated since the Pleistocene (Bigelow, 1967; Irving, 1967; Peterson, 1968; and Dumbleton, 1970). Bigelow stated that "the nearest relatives of the New Zealand alpine grasshoppers are apparently restricted to high cool habitats in both Tasmania and Chile...". The rearing experiments showed the grasshoppers to have a dependence on the alpine environment which would appear to

be physiological. It is, therefore, hypothesized that the New Zealand alpine grasshoppers are the descendents of a group which was alpine before the Pleistocene. The lengthening of their life cycle could have evolved when the alpine climate subsequently became milder. The New Zealand endemic grasshoppers may be members of the group Fleming (1963) refers to as "Old alpines with a long Tertiary history in the alpine zone of Antarctica that colonised New Zealand when the zone was first established in the Pliocene".

This discussion has shown that the New Zealand alpine grasshoppers are well adapted, and restricted to their alpine environment. No specific factor or factors restricting the grasshoppers to their environment were discovered, but the whole functioning of the animal appears to be intimately connected with the alpine environment.

Section 7

CONCLUSIONS

7.1 Summary

This study investigates aspects of the biology of five species of New Zealand alpine grasshoppers: Brachaspis collinus, Brachaspis nivalis, Paprides nitidus, Sigaus australis and Sigaus villosus. The first four species appear to be very similar in their general biology. Only limited information was obtained for Sigaus villosus.

All specimens examined were identified to species and instar. Eight instars are recorded which were assumed to exist but had not previously been found. Femur and pronotum length of most of the specimens examined were recorded. Analyses of these data are tabulated in the Appendix. They provide additional data on geographical variation in size and support previously proposed patterns of variation. Three morphologically aberrant specimens were found and are described.

The general structure of the grasshoppers, the structure of their alimentary canals, the structure of their gonads and their modes of copulation and oviposition follow the usual pattern for acridids. The structure of the male and female gonads of the five species studied are described. All the species lay egg pods, composed of eggs enveloped in froth, about 1 cm below the surface of the soil. The egg pods differ in detailed structure, but are similar in gross structure. None of the pods has a froth plug and all the grasshoppers leave a hole opening to the surface of

the soil following oviposition.

Femur and pronotum lengths, gonad structure and egg pod structure are used to compare different populations of the same species. Brachaspis nivalis populations at Porter Heights and Craigieburn are considered to be significantly different. The Paprides nitidus population at Temple Basin is considered to be different from those at Craigieburn and Porter Heights. The populations of Sigaus australis at Porter Heights and Craigieburn are not considered different and there were insufficient data available to compare the populations of Sigaus villosus at these two localities. The two scree inhabiting species Brachaspis nivalis and Sigaus villosus have similarities of form, colouring and egg pod structure which differentiate them from the other species.

Brachaspis collinus, Brachaspis nivalis, Paprides nitidus and Sigaus australis all appear to have a similar, flexible life cycle. All eggs go into an obligatory diapause which requires a cold period for termination. All stages including adults and eggs can overwinter and oviposition can occur at any time throughout the snow-free season. The instars follow the sequence proposed by Hudson (1970).

No method was discovered for successfully rearing grasshoppers in the laboratory or for predictably terminating diapause in their eggs.

Natural enemies of the grasshoppers are described. Six

parasitic species were found: an erythraeid mite, a tracheal mite, a mermithid, a cestode, a gregarine and a scelionid egg parasite. The first three parasites were found in sufficient numbers to permit a limited amount of work on their biology. These three were found throughout the snow-free season. Thus, like their grasshopper hosts they were not seasonal. Pipits were the only animals positively identified as predators on the grasshoppers. Potential predators are discussed.

The New Zealand alpine grasshoppers are shown to be well adapted to their environment. The basis of this adaptation appears to be their tolerance of winter cold. The New Zealand and Northern Hemisphere alpine grasshoppers differ in their adaptations to their respective environments. It is hypothesized that the egg diapause of the New Zealand alpine grasshoppers is a relic of a pre-Pleistocene alpine history.

7.2 Suggestions for Further Study

With more sophisticated environmental simulation equipment than was available during this study it should be possible to rear the grasshoppers in the laboratory. This would allow experiments to be conducted on the physiology of the animals, and permit more detailed studies of their development. The experiments conducted in the laboratory showed that egg diapause

could be terminated, but unfortunately a shortage of eggs and an uncertainty concerning their supply contrived to make experimental work difficult. If the grasshoppers could be reared or if large numbers of caged grasshoppers could be maintained, and thus a supply of eggs assured, a successful technique for the termination of egg diapause could be arrived at.

The parasites discussed in Section 5 warrant further research. Their apparent lack of seasonal distribution suggests either a long term association with the grasshoppers, or a ready facility for adapting to the life cycle of their hosts.

Because very little previous work has been done on the biology of the New Zealand alpine grasshoppers this study has, of necessity, been very broad in its coverage. It is hoped that this study provides basic information which can be used by subsequent workers as a basis for more detailed and critical studies of the New Zealand alpine grasshoppers.

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APPENDIX

List of Appendix Tables

Abbreviations used in Appendix Tables

S = standard deviation

V = coefficient of variation

K-S D max = maximum deviation from a normal frequency distribution as calculated by the Kolmogorov-Smirnov Test

N = number in sample

The term "All Areas" includes specimens collected from each of the study areas and may include individuals from the additional collections (Section 1.7).

Where N is less than five the measurement for each specimen is cited.

Table I: Femur and pronotum lengths of *Brachaspis collinus* from Temple Basin.

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	14.38703	14.28062	14.49343	0.58582	4.07187	0.05709	201
"	VI	12.17712	12.02909	12.32516	0.41875	3.43883	0.13898	57
"	V	9.73167	9.57293	9.89040	0.37589	3.86255	0.07015	41
"	IV	7.83249	7.67370	7.99128	0.30410	3.88258	0.15622	28
"	IIIA	6.26684	6.07388	6.45979	0.29398	4.69099	0.21399	19
"	II	4.70805	4.61005	4.80605	0.21585	4.58478	0.15376	36
"	I	3.58375	3.43343	3.73406	0.20584	5.74381	0.10277	16
Female	Adult	18.62460	18.48746	18.76173	0.66941	3.59421	0.05878	158
"	VI	15.40255	15.18736	15.61773	0.65369	4.24405	0.06300	65
"	V	12.35318	12.07502	12.63132	0.53269	4.31220	0.14699	28
"	IV	9.94439	9.69766	10.19112	0.44264	4.45119	0.13390	25
"	IIIB	7.86032	7.66944	8.05119	0.38646	4.91657	0.10976	31
"	IIIA	6.15499	6.07165	6.23834	0.11413	1.85433	0.14245	16
"	II	4.78124	4.61651	4.94598	0.28854	6.03480	0.17366	24
"	I	3.56600	3.46767	3.66432	0.12922	3.62360	0.13255	15

(b) Pronotum length:

Male	Adult	4.83327	4.79722	4.86932	0.20384	4.21734	0.07897	212
"	VI	4.44447	4.38664	4.50230	0.16557	3.72538	0.12965	58
"	V	3.55074	3.48566	3.61583	0.15224	4.28748	0.10406	40
"	IV	2.80624	2.70397	2.90851	0.17912	6.38304	0.18981	24
"	IIIA	2.18618	2.04192	2.33045	0.23353	10.68193	0.33355	21
"	II	1.57514	1.53096	1.61932	0.09596	6.09207	0.10669	35
"	I	1.14300	1.06647	1.21952	0.10479	9.16814	0.09554	16
Female	Adult	6.42874	6.37165	6.48584	0.28307	4.40326	0.07685	163
"	VI	5.54909	5.47358	5.62460	0.23687	4.26864	0.07964	69
"	V	4.47517	4.37422	4.57611	0.19724	4.40747	0.13056	29
"	IV	3.55268	3.47076	3.63461	0.15032	4.23119	0.08018	26
"	IIIB	2.75266	2.68107	2.82425	0.14259	5.17990	0.12578	30
"	IIIA	2.11666	2.05845	2.17487	0.07650	3.61422	0.15219	15
"	II	1.60291	1.55270	1.65312	0.08795	5.48666	0.10387	24
"	I	1.21214	1.05966	1.36462	0.19164	15.81001	0.39145	14

Table II: Femur and pronotum lengths of Brachaspis nivalis from Craigieburn.

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	11.52894	11.08982	11.96806	0.66902	5.80296	0.24120	19
"	VI	10.15285	9.27405	11.03164	0.66450	6.54494	0.11514	7
"	V	8.16999	6.92464	9.41535	0.69065	8.45351	0.22142	5
"	IV	6.95, 6.92, 6.4						3
"	IIIA	5.12						1
"	II	4.29, 4.48						2
"	I	No data						
Female	Adult	15.26466	14.93180	15.59751	0.71250	4.66763	0.14032	34
"	VI	12.75714	10.95130	14.56298	1.36548	10.70362	0.16307	7
"	V	10.34999	9.53193	11.16805	0.61857	5.97656	0.24167	7
"	IV	8.8, 8.65						2
"	IIIB	6.84399	6.42622	7.26177	0.23169	3.38529	0.17530	5
"	IIIA	6.35, 5.63						2
"	II	No data						
"	I	No data						

(b) Pronotum length:

Male	Adult	3.80750	3.65847	3.95651	0.23425	6.15229	0.10328	20
"	VI	3.51000	3.21021	3.80978	0.19809	5.64362	0.18879	6
"	V	2.65, 3.0, 3.1, 2.8						4
"	IV	2.55, 2.25, 2.35, 2.45						4
"	IIIA	1.92, 1.84						2
"	II	1.4, 1.52						2
"	I	No data						
Female	Adult	5.10222	4.97809	5.22634	0.27340	5.35851	0.07579	36
"	VI	4.43428	4.05597	4.81259	0.28606	6.45103	0.19517	7
"	V	3.66142	3.49705	3.82560	0.12429	3.39454	0.10805	7
"	IV	3.09, 3.13						2
"	IIIB	2.41800	2.27636	2.55964	0.07855	3.24852	0.28984	5
"	IIIA	2.05, 1.94						2
"	II	1.54						1
"	I	No data						

Table III: Femur and pronotum lengths of Brachaspis nivalis from Porter Heights.

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	10.72910	10.45244	11.00576	0.60087	5.60036	0.11931	35
"	VI	9.5, 9.4, 8.45						3
"	V	7.77799	6.73205	8.82394	0.58006	7.45770	0.37385	5
"	IV	6.27999	5.94622	6.61377	0.33307	5.30361	0.18802	10
"	IIIA	5.24333	5.16344	5.32322	0.05279	1.00678	0.33740	6
"	II	No data						
"	I	3.13, 3.15, 3.17						3
Female	Adult	14.60760	14.36116	14.85404	0.71764	4.91282	0.09365	60
"	VI	12.03749	11.58697	12.48801	0.51085	4.24381	0.12493	12
"	V	9.7, 9.7, 9.4						3
"	IV	8.60999	8.27025	8.94974	0.18841	2.18832	0.15662	5
"	IIIB	6.51999	6.01158	7.02841	0.28196	4.32450	0.26479	5
"	IIIA	5.83, 5.17, 5.4						3
"	II	4.15, 4.55						2
"	I	3.07						1

(b) Pronotum length:

Male	Adult	3.63913	3.56055	3.71771	0.17066	4.68965	0.07877	35
"	VI	3.42, 3.17, 3.25						3
"	V	2.85600	2.21726	3.49474	0.35423	12.40306	0.36281	5
"	IV	2.30222	2.17383	2.43060	0.11851	5.14761	0.13914	9
"	IIIA	1.94, 1.84, 1.83, 1.64						4
"	II	No data						
"	I	1.073, 1.15, 1.13						3
Female	Adult	4.90429	4.81971	4.98886	0.25692	5.23860	0.09369	65
"	VI	4.24727	4.12037	4.37417	0.13551	3.19042	0.13416	11
"	V	3.58, 3.37, 3.37						3
"	IV	3.13800	3.02017	3.25583	0.06535	2.08238	0.25097	5
"	IIIB	2.31000	2.02920	2.59080	0.15572	6.74130	0.2499	5
"	IIIA	2.04, 1.85, 1.9						3
"	II	1.23, 1.535						2
"	I	1.02						1

Table IV: Femur and pronotum lengths of Brachaspis nivalis from All Areas.

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	11.06501	10.82142	11.30861	0.71282	6.44214	0.08816	61
"	VI	9.87454	9.16798	10.58110	0.75447	7.64056	0.07701	11
"	V	7.97399	7.33685	8.61113	0.63579	7.97327	0.18372	10
"	IV	6.38999	6.07428	6.70571	0.37793	5.91444	0.18175	13
"	IIIA	5.22571	5.13704	5.31438	0.06705	1.28301	0.24822	7
"	II	4.29, 4.48						2
"	I	3.13, 3.15, 3.17						3
Female	Adult	14.80407	14.58314	15.02499	0.83740	5.65653	0.08015	99
"	VI	12.30262	11.67712	12.92813	0.95299	7.74621	0.16698	19
"	V	10.12499	9.49676	10.75323	0.62690	6.19162	0.29791	10
"	IV	8.64285	8.41884	8.86686	0.16938	1.95980	0.17676	7
"	IIIB	6.68199	6.38412	6.97987	0.29724	4.44836	0.12862	10
"	IIIA	5.67599	4.86341	6.48858	0.45064	7.93947	0.16627	5
"	II	4.15, 4.55						2
"	I	3.07						1

(b) Pronotum length:

Male	Adult	3.70036	3.62459	3.77613	0.21054	5.68962	0.08320	55
"	VI	3.43333	3.21178	3.65489	0.20451	5.95665	0.18723	9
"	V	2.87000	2.56695	3.17304	0.27973	9.74677	0.26546	9
"	IV	2.33230	2.22751	2.43710	0.12544	5.37849	0.08499	13
"	IIIA	1.83500	1.67434	1.99566	0.10616	5.78530	0.16131	6
"	II	1.4, 1.52						2
"	I	1.073, 1.15, 1.13						3
Female	Adult	4.95854	4.88488	5.03219	0.28888	5.82598	0.06122	106
"	VI	4.31999	4.17063	4.46936	0.22019	5.09693	0.08039	18
"	V	3.59499	3.43653	3.75346	0.15813	4.39865	0.12261	10
"	IV	3.13000	3.05557	3.20442	0.05627	1.79787	0.18995	7
"	IIIB	2.36400	2.23426	2.49373	0.12946	5.47633	0.11072	10
"	IIIA	1.95600	1.79849	2.11351	0.08735	4.46574	0.17267	5
"	II	1.23, 1.535, 2.05, 1.94						4
"	I	1.02, 1.54						2

Table V: Femur and pronotum lengths of Paprides nitidus from Craigieburn.

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	10.32199	9.91646	10.72753	0.53296	5.16333	0.13953	15
"	VI	8.8						1
"	V	7.3						1
"	IV	5.83, 5.88, 5.35, 5.52						4
"	IIIA	not present in species						
"	II	4.25000	4.04010	4.45989	0.11640	2.73893	0.16555	5
"	I	3.36, 3.26						2
Female	Adult	15.19687	14.27498	16.11876	1.26243	8.30717	0.15704	16
"	VI	12.35, 11.78						2
"	V	9.97						1
"	IV	No data						
"	IIIB	5.76221	5.53466	5.98976	0.21005	3.64524	0.29103	9
"	IIIA	not present in species						
"	II	4.49272	4.24311	4.74233	0.26654	5.93263	0.06747	11
"	I	No data						

(b) Pronotum length:

Male	Adult	3.58499	3.41909	3.75090	0.22719	6.33712	0.13285	16
"	VI	3.23						1
"	V	2.75						1
"	IV	1.91, 2.15, 1.74, 2.0						4
"	IIIA	not present in species						
"	II	1.48300	1.35397	1.61202	0.07155	4.82496	0.27766	5
"	I	1.09, 1.01						2
Female	Adult	5.13444	4.89525	5.37363	0.35261	6.86749	0.13097	18
"	VI	4.5, 4.14						2
"	V	3.52						1
"	IV	No data						
"	IIIB	1.93643	1.82786	2.04500	0.08209	4.23942	0.21937	7
"	IIIA	not present in species						
"	II	1.45564	1.37622	1.53505	0.08480	5.82538	0.11260	11
"	I	No data						

Table VI: Femur and pronotum lengths of Paprides nitidus from Porter Heights.

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	10.40677	10.18921	10.62433	0.53647	5.15504	0.13324	44
"	VI	8.85884	8.68438	9.03330	0.32010	3.61338	0.14869	26
"	V	7.9, 7.00, 7.06, 7.2						4
"	IV	6.35						1
"	IIIA	not present in species						
"	II	No data						
"	I	3.1						1
Female	Adult	15.26206	15.04044	15.48368	0.65072	4.26367	0.10458	61
"	VI	11.89843	11.52392	12.27293	0.68716	5.77522	0.15573	26
"	V	9.57954	9.31940	9.83967	0.43282	4.51822	0.20857	22
"	IV	7.37, 7.99, 7.36, 7.55						4
"	IIIB	No data						
"	IIIA	not present in species						
"	II	No data						
"	I	No data						

(b) Pronotum length:

Male	Adult	3.65045	3.59929	3.70161	0.12616	3.45598	0.13467	44
"	VI	3.25079	3.15770	3.34388	0.16701	5.13739	0.20573	25
"	V	2.77400	2.28206	3.26593	0.27282	9.83484	0.26197	5
"	IV	2.36						1
"	IIIA	not present in species						
"	II	No data						
"	I	0.99						1
Female	Adult	5.23950	5.15307	5.32592	0.25584	4.88288	0.13150	62
"	VI	4.21922	4.05679	4.38166	0.29804	7.06397	0.21692	26
"	V	3.38363	3.28970	3.47756	0.15628	4.61878	0.13527	22
"	IV	No data						
"	IIIB	No data						
"	IIIA	not present in species						
"	II	No data						
"	I	No data						

Table VII: Femur and pronotum lengths of Paprides nitidus from Temple Basin.

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	10.63734	10.53371	10.74097	0.28533	2.68232	0.11143	54
"	VI	8.9						1
"	V	7.41						1
"	IV	5.78857	5.63502	5.94212	0.11611	2.00581	0.21775	7
"	IIIA	not present in species						
"	II	4.42, 4.40						2
"	I	3.48						1
Female	Adult	15.18073	15.05036	15.31110	0.52326	3.44688	0.07325	111
"	VI	12.40454	12.00422	12.80486	0.42747	3.44604	0.12321	11
"	V	No data						
"	IV	7.62200	6.99588	8.24811	0.34723	4.55565	0.24502	5
"	IIIB	5.95600	5.65627	6.25572	0.16622	2.79084	0.13823	5
"	IIIA	not present in species						
"	II	No data						
"	I	No data						

(b) Pronotum length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	3.73092	3.66182	3.80001	0.19023	5.09887	0.15455	54
"	VI	3.26						1
"	V	2.65						1
"	IV	1.98, 1.95, 2.00, 1.95						4
"	IIIA	not present in species						
"	II	No data						
"	I	No data						
Female	Adult	5.19029	5.14110	5.23949	0.19983	3.85005	0.09560	113
"	VI	4.22299	3.93841	4.50758	0.28398	6.72465	0.18644	10
"	V	No data						
"	IV	2.66000	2.50229	2.81771	0.08746	3.28814	0.12371	5
"	IIIB	2.03600	1.90560	2.16640	0.07232	3.55200	0.18809	5
"	IIIA	not present in species						
"	II	No data						
"	I	No data						

Table VIII: Femur and pronotum lengths of Paprides nitidus from All Areas

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	10.48681	10.38073	10.59289	0.44772	4.26939	0.09457	206
"	VI	8.85821	8.69721	9.01920	0.30833	3.48071	0.14503	28
"	V	7.31166	6.81946	7.80386	0.32523	4.44814	0.21452	6
"	IV	5.79214	5.60851	5.97576	0.23079	3.98455	0.14913	14
"	IIIA	not present in species						
"	II	4.29571	4.13287	4.45855	0.12313	2.86643	0.15640	7
"	I	3.48, 3.36, 3.26, 3.1						4
Female	Adult	15.15234	15.01648	15.28820	0.75729	4.99782	0.11221	206
"	VI	12.08183	11.81795	12.34571	0.63244	5.23467	0.11113	42
"	V	9.59651	9.34446	9.84857	0.43064	4.48746	0.18765	23
"	IV	7.51636	7.20606	7.82665	0.33134	4.40823	0.15986	11
"	IIIB	5.80266	5.62562	5.97970	0.23267	4.00971	0.17098	15
"	IIIA	not present in species						
"	II	4.49272	4.24311	4.74233	0.26654	5.93263	0.06747	11
"	I	No data						

(b) Pronotum length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	3.67425	3.63261	3.71589	0.17647	4.80281	0.12493	123
"	VI	3.25036	3.16476	3.33596	0.16052	4.93838	0.17318	27
"	V	2.75285	2.45198	3.05372	0.22750	8.26421	0.22984	7
"	IV	2.00363	1.85914	2.14812	0.15429	7.70050	0.23667	11
"	IIIA	not present in species						
"	II	1.48300	1.35397	1.61202	0.07155	4.82496	0.27766	5
"	I	0.99						1
Female	Adult	5.18049	5.13704	5.22394	0.24454	4.72034	0.11388	210
"	VI	4.24316	4.12300	4.36333	0.28455	6.70600	0.14885	41
"	V	3.38363	3.28970	3.47756	0.15628	4.61878	0.13527	22
"	IV	2.60857	2.42895	2.78819	0.13582	5.20676	0.11439	7
"	IIIB	1.99423	1.83967	2.14879	0.18502	9.27781	0.21384	13
"	IIIA	not present in species						
"	II	1.45564	1.37622	1.53505	0.08480	5.82538	0.11260	11
"	I	No data						

Table IX: Femur and pronotum lengths of Sigaus australis from Craigieburn.

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	11.35, 10.95, 11.6, 11.5						4
"	VI	9.1						1
"	V	No data						
"	IV	No data						
"	IIIA	not present in species						
"	II	4.05, 4.2						2
"	I	3.28200	3.05024	3.51376	0.12853	3.91622	0.28823	5
Female	Adult	17.93999	16.07216	19.80780	1.03586	5.77400	0.31540	5
"	VI	No data						
"	V	10.15						1
"	IV	No data						
"	IIIB	No data						
"	IIIA	not present in species						
"	II	4.25, 4.45, 4.30						3
"	I	No data						

(b) Pronotum length:

Male	Adult	3.46, 3.50, 3.16, 3.46						4
"	VI	3.07						1
"	V	No data						
"	IV	No data						
"	IIIA	not present in species						
"	II	No data						
"	I	1.087						1
Female	Adult	5.57833	5.23052	5.92613	0.22982	4.11985	0.16738	6
"	VI	No data						
"	V	3.2						1
"	IV	No data						
"	IIIB	No data						
"	IIIA	not present in species						
"	II	1.43						1
"	I	No data						

Table X: Femur and pronotum lengths of Sigaus australis from Porter Heights.

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	11.42812	10.18262	11.96154	0.73046	6.39180	0.17555	16
"	VI	9.32608	9.07490	9.57726	0.38809	4.16136	0.22244	23
"	V	7.10, 8.90, 7.05, 7.78						4
"	IV	No data						
"	IIIA	not present in species						
"	II	No data						
"	I	3.26, 3.2						2
Female	Adult	17.99223	17.79434	18.19011	0.66249	3.68209	0.07317	78
"	VI	14.12368	13.44585	14.80150	1.03271	7.31189	0.09552	19
"	V	10.99999	10.47219	11.52779	0.59848	5.44076	0.09066	12
"	IV	8.38300	7.49737	9.26862	0.88374	10.54208	0.17762	10
"	IIIB	6.48400	5.39121	7.57678	0.60604	9.34664	0.22097	5
"	IIIA	not present in species						
"	II	No data						
"	I	3.18						1

(b) Pronotum length:

Male	Adult	3.42222	3.30513	3.53931	0.17261	5.04385	0.20224	18
"	VI	3.06681	2.94681	3.18682	0.19968	6.51084	0.13104	22
"	V	2.66, 2.55, 3.17, 2.46						4
"	IV	No data						
"	IIIA	not present in species						
"	II	No data						
"	I	1.14, 1.073						2
Female	Adult	5.49154	5.41895	5.56412	0.24915	4.53704	0.06691	82
"	VI	4.58105	4.44664	4.71545	0.20477	4.47001	0.09452	19
"	V	3.71769	3.53803	3.89753	0.21506	5.78488	0.19967	13
"	IV	2.84099	2.59963	3.08236	0.24085	8.47750	0.21491	10
"	IIIB	2.15, 2.13, 2.25, 2.05						4
"	IIIA	not present in species						
"	II	No data						
"	I	1.053						1

Table XI: Femur and pronotum lengths of Sigaus australis from All Areas.

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	11.42142	11.02341	11.81944	0.64427	5.64088	0.20035	21
"	VI	9.31666	9.09836	9.53496	0.38236	4.10401	0.22571	24
"	V	7.10, 8.90, 7.05, 7.78						4
"	IV	No data						
"	IIIA	not present in species						
"	II	4.05, 4.20						2
"	I	3.26714	3.12253	3.41175	0.10935	3.34693	0.20385	7
Female	Adult	17.96545	17.77304	18.15785	0.68213	3.79692	0.05945	87
"	VI	14.12368	13.44585	14.80150	1.03271	7.31189	0.09552	19
"	V	10.93461	10.41700	11.45221	0.61960	5.66645	0.08125	13
"	IV	8.38300	7.49737	9.26862	0.88374	10.54208	0.17762	10
"	IIIB	6.48400	5.39121	7.57678	0.60604	9.34664	0.22097	5
"	IIIA	not present in species						
"	II	4.25, 4.45, 4.30						3
"	I	3.18						1

(b) Pronotum length:

Male	Adult	3.42391	3.32677	3.52104	0.16596	4.84712	0.15029	23
"	VI	3.06681	2.94681	3.18681	0.19968	6.50840	0.13104	22
"	V	2.66, 2.55, 3.17, 2.46						4
"	IV	No data						
"	IIIA	not present in species						
"	II	No data						
"	I	1.087, 1.14, 1.073						3
Female	Adult	5.48570	5.41657	5.55484	0.25205	4.59461	0.06428	92
"	VI	4.58105	4.44664	4.71545	0.20477	4.47001	0.09452	19
"	V	3.66642	3.46402	3.86883	0.25440	6.93851	0.16413	14
"	IV	2.84099	2.59963	3.08236	0.24085	8.47750	0.21491	10
"	IIIB	2.15, 2.13, 2.25, 2.05						4
"	IIIA	not present in species						
"	II	1.43						1
"	I	1.053						1

Table XII: Femur and pronotum lengths of Sigaus villosus from Craigieburn.

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	15.94000	15.21200	16.66798	0.40373	2.53282	0.23561	5
"	VI	13.40						1
"	V	11.65, 10.30, 11.30						3
"	IV	8.80						1
"	IIIA	6.70						1
"	II	5.30, 5.22, 5.52, 5.40						4
"	I	No data						
Female	Adult	21.31248	20.59953	22.02542	0.60104	2.82014	0.19212	8
"	VI	16.60, 16.50						2
"	V	14.35						1
"	IV	12.20						1
"	IIIB	No data						
"	IIIA	6.85						1
"	II	No data						
"	I	No data						

(b) Pronotum length:

Male	Adult	5.39600	4.81232	5.97968	0.32370	5.99884	0.23487	5
"	VI	4.80						1
"	V	4.20, 4.20, 4.10						3
"	IV	3.07						1
"	IIIA	2.40						1
"	II	1.74, 1.74, 1.84, 1.74						4
"	I	No data						
Female	Adult	7.39624	7.07357	7.71891	0.27203	3.67789	0.30371	8
"	VI	6.55, 6.20						2
"	V	5.12						1
"	IV	4.30						1
"	IIIB	No data						
"	IIIA	2.28						1
"	II	No data						
"	I	No data						

Table XIII: Femur and pronotum lengths of Sigaus villosus from Porter Heights.

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of Mean		S	V	K-S D max	N
Male	Adult	15.73888	15.26375	16.21400	0.43859	2.78664	0.17980	9
"	VI	14.10						1
"	V	No data						
"	IV	8.23, 8.40						2
"	IIIA	No data						
"	II	5.27						1
"	I	No data						
Female	Adult	20.77301	20.46143	21.08458	0.57171	2.75215	0.07644	26
"	VI	No data						
"	V	No data						
"	IV	No data						
"	IIIB	No data						
"	IIIA	No data						
"	II	No data						
"	I	No data						

(b) Pronotum length:

Male	Adult	5.32250	5.20992	5.43507	0.12764	2.39821	0.11650	12
"	VI	4.80, 5.15						2
"	V	No data						
"	IV	2.86, 3.17						2
"	IIIA	No data						
"	II	1.86						1
"	I	No data						
Female	Adult	7.25285	7.11690	7.38880	0.26035	3.58967	0.09619	28
"	VI	No data						
"	V	No data						
"	IV	No data						
"	IIIB	No data						
"	IIIA	No data						
"	II	No data						
"	I	No data						

Table XIV: Femur and pronotum lengths of Sigaus villosus from All Areas.

(a) Femur length:

Sex	Instar	Mean (mm)	99% Conf. limits of mean		S	V	K-S D max	N
Male	Adult	15.81071	15.47453	16.14688	0.42253	2.67240	0.11957	14
"	VI	13.40, 14.10						2
"	V	11.65, 10.30, 11.30						3
"	IV	8.80, 8.23, 8.40						3
"	IIIA	6.70						1
"	II	5.43420	5.12697	5.55702	0.11925	2.23227	0.23766	5
"	I	No data						
Female	Adult	20.85937	20.53105	21.18768	0.73313	3.51462	0.06876	37
"	VI	16.60, 16.50						2
"	V	14.35						1
"	IV	12.20						1
"	IIIB	No data						
"	IIIA	6.85						1
"	II	No data						
"	I	No data						

(b) Pronotum length:

Male	Adult	5.34411	5.20604	5.48218	0.19644	3.67580	0.09568	17
"	VI	4.80, 5.15, 4.80						3
"	V	4.20, 4.20, 4.10						3
"	IV	2.86, 3.17, 3.07						3
"	IIIA	2.4						1
"	II	1.77200	1.68898	1.85502	0.04604	2.59837	0.35647	5
"	I	No data						
Female	Adult	7.27229	7.14608	7.39850	0.29148	4.00807	0.09288	39
"	VI	6.55, 6.20						2
"	V	5.12						1
"	IV	4.30						1
"	IIIB	No data						
"	IIIA	2.28						1
"	II	No data						
"	I	No data						

Table XV: Number of follicles* in testes of adult male grasshoppers.

Species and Study Area	Mean	95% Confidence limits of mean		S	V	K-S D max	N
Brachaspis collinus							
Temple Basin	109.83333	105.46222	114.20442	8.82676	8.03649	0.09396	18
Brachaspis nivalis							
Craigieburn	No data						
Porter Heights	46.59999	42.10257	51.09740	3.91152	8.39382	0.19236	5
Paprides nitidus							
Craigieburn	53, 61						2
Porter Heights	62.5000	56.69762	68.30237	3.83406	6.13449	0.15219	6
Temple Basin	53, 50, 64						3
All Areas	59.50000	53.50117	65.49881	5.98609	10.06066	0.16123	10
Sigaus australis							
Craigieburn	No data						
Porter Heights	26, 26, 23, 28						4
Sigaus villosus							
Craigieburn	No data						
Porter Heights	68, 86, 87						3

* Number of follicles is the number of follicles per individual NOT per individual testis

Table XVI: Length of egg pods (in mm) laid in the laboratory.

Species and Study Area	Mean	95% Confidence limits of mean		S	V	K-S D max	N
Brachaspis collinus							
Temple Basin	22.48929	21.70456	23.27400	2.67120	11.87764	0.08577	47
Brachaspis nivalis							
Craigieburn	16.03333	14.66840	17.39824	2.48068	15.47205	0.17151	15
Porter Heights	13.37999	12.05156	14.70843	1.88550	14.09191	0.10926	10
All Areas	15.00380	13.98040	16.02719	2.53810	16.91638	0.09684	26
Paprides nitidus							
Craigieburn	12.0, 12.6						2
Porter Heights	12.10999	10.55626	13.66373	2.20527	18.21033	0.13575	10
Temple Basin	15.62000	14.63292	16.60707	0.85849	5.49607	0.25806	5
All Areas	12.87894	11.65532	14.10256	2.54833	19.78676	0.08214	19
Sigaus australis							
Craigieburn	No data						
Porter Heights	15.0, 18.9, 20.4						3
Sigaus villosus							
Craigieburn	28.0, 31.4						2
Porter Heights	No data						

Table XVII: Number of eggs per pod, for egg pods laid in the laboratory.

Species and Study Area	Mean	95% Confidence limits of mean		S	V	K-S D max	N
Brachaspis collinus							
Temple Basin	34.14516	32.65849	35.63181	5.85296	17.14140	0.11506	62
Brachaspis nivalis							
Craigieburn	12.23809	10.40050	14.07568	4.04851	33.08119	0.19012	21
Porter Heights	9.83333	8.11268	11.55398	1.72240	17.51593	0.12812	6
All Areas	11.62069	10.23499	13.00639	3.64900	31.40089	0.21722	29
Paprides nitidus							
Craigieburn	21, 21						2
Porter Heights	16.39999	12.23576	20.56422	5.91044	36.03928	0.20669	10
Temple Basin	23.00000	19.57668	26.42331	3.82971	16.65089	0.13758	7
All Areas	18.95238	16.26912	21.63562	5.91165	31.19211	0.16988	21
Sigaus australis							
Craigieburn	No data						
Porter Heights	27, 24, 28, 32						4
Sigaus villosus							
Craigieburn	24						1
Porter Heights	No data						